

Osteology of the Soay sheep

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17 MAY 1990

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This project describes the elements of the skeleton of a single breed of sheep, the Soay, using a large sample of more than 60 skeletons and more than 1000 randomly collected bones derived from a single population. It has involved field observation and field collection on the island of Hirta, St. Kilda, Scotland; the maintenance of a small flock at Cambridge, and skeletal preparation, measurement, qualitative assessment and curation in the British Museum (Natural History). In addition, for comparison, a number of goat skeletons were collected from Holy Island, Arran, Scotland. Despite the use of the Soay as a model of primitive domestic sheep for comparison with modern breeds, and with the remains of prehistoric sheep from archaeological sites, no metrical or morphological analysis of the

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Two Soay sheep photographed at Laundry Farm, Cambridge, in December 1982. Both are three and a half years old. Left: entire ram, light, wild-type colour of fleece; right: male castrate, dark, wild-type fleece.

Soay skeleton has previously been undertaken. Here comparisons and deductions are presented concerning the status of the Soay as a model. A further important part of the project relates to the interpretation of bone collections recovered from archaeological sites where to distinguish sheep from goats aids the reconstruction of palaeoeconomy and palaeoecology. We have examined the anatomical criteria by which the bones of the Soay can be distinguished from those of goats, using the characters that were first observed by Gromova and by Boessneck and his colleagues. The question is whether primitive breeds, that are likely to be similar to the sheep represented on archaeological sites, exhibit the appropriate anatomical features. Rather few totally reliable features could be verified but sets of features are diagnostic. Criteria for distinguishing sex from certain bones were substantiated. The effects of castration of the male on bone and horn development are described and the genetics of hornedness are discussed. The bones have been incorporated into the national collection, and the data base is held as an archive at the British Museum (Natural History).

INTRODUCTION

Historical background

The Soay sheep occupies a special position in the mammalian fauna of Europe. It is derived from domesticated stock but retains many features of wild sheep and until the end of the nineteenth century it survived only as a feral population, of about 200 animals, on the tiny island of Soay in the St Kilda archipelago of the Outer Hebrides, Scotland. The main island of St Kilda is Hirta and this was inhabited until August 1930 when the islanders were evacuated together with their stock. This left the island of Hirta free of livestock until 1932 when the landowner, the Marquess of Bute, transferred 107 Soay sheep of mixed age and sex from the island of Soay to the newly deserted main island. Soay sheep have lived wild on Hirta since that time and for the last 30 years detailed studies have been carried out on their ecology and reproductive behaviour (Jewell, Milner & Boyd, 1974; Jewell, 1986).

The origins of the Soay sheep are unknown but its small slender bones and the structure of the fleece, which closely resembles some finds of prehistoric cloth, suggest that it may be a relic of the sheep that were widespread through Europe in the Bronze Age, around 3500 years before present (Ryder, 1983, p. 47). It is not known when sheep were first taken to the island of Soay; it could have been in the prehistoric period, or in early Christian times when there was much movement in the region, or they could have been taken there by the Vikings. The word 'Soay' or 'Soa' means 'island of sheep' in old Norse, so perhaps there were already sheep on the island when the Norsemen first arrived there.

The sheep on Soay had no contact with humans except when the islanders landed about once a year to catch sea birds. A few sheep were occasionally removed and a number were brought to England at the beginning of this century. They were described by the well known naturalist, H. J. Elwes, in 1913, and he sent some to the Duke of Bedford at Woburn Abbey (Elwes, 1913). From that time the Soay sheep became well known as park animals and today there are about 4000 Soays on farms and parks throughout Britain.

Although classified as a domestic sheep, *Ovis aries* L., the Soay has great zoological interest in representing an early stage in the evolution of modern commercial sheep from the wild ancestor, *Ovis orientalis* Gmelin, 1774 (Clutton-Brock, 1987).

The distinctive features of the Soay sheep, its short tail, brown colouring, annually moulting coat and, typically, large black horns in the male, are characters shared with wild sheep. It is known, however, that wild sheep were not present in Europe in post-glacial times and that they were brought

there as domesticated animals from western Asia in the late Mesolithic and early Neolithic. These sheep probably differed little from the wild species but with poor feeding and the stress of captivity they soon became much reduced in size so that their bones, recovered from archaeological sites, closely resemble those of the present day Soay. As long ago as 1931, D. M. S. Watson likened the abundant sheep remains from the late Neolithic site of Skara Brae on Orkney to the bones of the Soay (Childe, 1931).

The Soay is very similar in body proportions, coloration, and fleece to the mouflon *Ovis musimon* Pallas, 1811, of Corsica and Sardinia except that it is a rather smaller animal. The average weight of the Soay for males in good condition is 36 kg and 25 kg for females, while a mouflon has a maximum weight of about 55 kg (Jewell *et al.*, 1974, p. 88). The Soay has two colour phases, a dark form which is closely similar to the colour of the mouflon, and a light form which is beige-brown in colour. There are also two types of fleece which correspond to those described for textiles as 'hairy medium' and 'generalized medium' (Ryder, 1983, p. 47); that is they can be hairy or woolly. The fleece is self-shedding in the early summer as in wild sheep, in the mouflon and in some other primitive breeds.

The Corsican and Sardinian mouflon used to be considered as a relic of an endemic wild species, but it is now realized that, as there are no authentic Pleistocene fossils of sheep from the Mediterranean region, the mouflon, like the Soay, must be an anciently feral sheep that was introduced in the prehistoric period (Poplin, 1979). It has survived in its very primitive form on Corsica and Sardinia because it has never interbred with improved stock. Ryder (1983, p. 48) considers that the mouflon has a fleece that is very little altered from that of the wild sheep.

The Soay sheep is the smallest and one of the last relict populations of primitive domestic sheep that survived from the prehistoric period until the last century in the western and northern isles of Britain, in Iceland, and in Scandinavia, as well as in the highlands of Scotland. Ryder (1983) regards some of these sheep, for example the Orkney sheep from North Ronaldsay, as survivals of a late Iron Age type because their fleece is rather more developed than it is in the Soay. However, sheep similar to the Soay did survive on the smallest of the Faroe islands, known as Little Dimun, until the year 1865 (Hatting, 1983). Historical references to these sheep are cited in Jewell (1980).

The study of the feral Soay sheep on the island of Hirta was begun in 1959 and still continues. Since then a sample of the lambs born every spring has been given coloured and numbered ear tags. Carcasses of animals of known age are therefore frequently encountered during field work. The sheep often die in the shelter of dry stone chambers known

as cleits, and then become mummified, so preserving the skeleton intact.

Events in the life cycle of the Soay on Hirta follow a strict annual cycle. The great majority of adult deaths occur in March, after the rigours of winter when grazing is at a minimum. Almost all lambs are born within a fortnight in April, so that births and deaths are close together in time and the sheep live for a given number of whole years (Jewell *et al.*, 1974, p. 364). As J. Morton Boyd has written (in Jewell *et al.*, 1974), 'in winter and spring both people and sheep on St Kilda were in a state of distress through malnutrition. This inexorable cycle of winter poverty and summer recovery to which the Soay sheep today are subject was at the heart of the problem of human survival at St Kilda since it first became settled by humans'.

The osteological study

The collection of Soay sheep bones from Hirta provides a large number of skeletal elements from a single, reproductively isolated population in which variation is individual and sexual but is unaffected by artificial selection and breed differences. The material is therefore ideal for the categorization of osteological features specific to sheep, which can be used to distinguish the remains of sheep from those of goats in assemblages retrieved from archaeological sites. Hence it was appropriate for a large part of this osteological study to be devoted to the definition of sheep-specific characters in the Soay material.

Bones of the Soay sheep have been used for nearly a hundred years, since first measured by Pitt Rivers (1898), for the identification, ageing, and general description of the remains of sheep from archaeological sites, and yet the skeleton of the Soay itself has never been described osteologically, nor its elements quantified. Recently, however, two projects have been undertaken to establish the parameters of the Soay skeleton, one being the present work on material collected from feral sheep on Hirta and the second project being an analysis by S. Payne and A. J. Legge of skeletal material from mainland 'park' Soays bred at the Agricultural and Food Research Council Institute of Animal Physiology at Babraham, Cambridge. No previous large-scale metrical analyses of the skeletons of a single breed of sheep have been carried out. The nomenclature of the bones throughout the work follows that of Hughes & Dransfield (1953).

MATERIALS AND METHODS

Collection of the material

Soay sheep skeletons and bones

The population of Soay sheep on the island of Hirta goes through cycles of 'boom and bust' producing heavy mortality in certain years. In the winter of 1978/79 there was very heavy mortality and 224 tagged and therefore known-age sheep were counted dead. A selection of these was stored in the cleits and 47 skeletons later shipped back to the British Museum (Natural History) to be added to the collection that already existed.

Over the years, between 1959 and 1978, a collection of over a thousand separate bones, picked up at random, was also

made. Long bones of the appendicular skeleton with fused epiphyses, skulls, mandibles, and scapulae predominated in this collection. (It should be noted that in the years 1978, 1979 and 1980, 72 male sheep on Hirta were castrated (Jewell, 1986) but the *random* collection of bones was made before any dead castrates could have contributed to this material. Two one-year old castrate *skeletons* collected in 1979, were, however, added to our study material.)

In a small flock of Soay sheep originally maintained at the Royal Holloway College (London University), 7 male lambs were castrated shortly after birth. The sheep in this flock were derived from an importation of animals direct from Hirta in 1963. They were later moved to the University of Cambridge where they were killed to give a series of known ages up to nine years old (see Table 1), and the skeletons were presented to the British Museum (Natural History). To these was added the skeleton of a castrate aged 6 years 4 months from Babraham, which had been presented to the British Museum (Natural History), to increase the size of the sample. It was considered permissible to include this skeleton in the analysis because its size was within the range of the other castrates and it had been raised under similar grazing conditions.

Soay sheep horns and horn cores

Information and measurements on the horns and horn cores of the Soay sheep were obtained from the following sources:

1. Measurements were recorded in the field, on Hirta, of over 80 known-age sheep that had died in the spring of 1979. Where possible the horn sheaths were pulled off to allow measurement of the horn cores. Only the horn sheaths of these individuals were collected, not the skulls or skeletons.
2. Visual inspection was made of the growth of the horns on 44 living adults with lambs at foot, on Hirta, in 1980.
3. Records of the annual incremental growth in the horns of the 7 castrated Soays kept at Cambridge were made through 1978–81. After these animals had been killed their horn sheaths were pulled off and the horn cores were measured (see Appendix).
4. Measurements were taken in the British Museum (Natural History) of the horn cores from the collection of cleaned skulls (see Appendix).

Goats

The goat material used in the study was collected in 1982 from a feral flock on Holy Island, Arran, Scotland, by Sheila Cameron who very kindly presented 7 skeletons to the Museum.

The metrical analysis

The parts of the skeleton that were used in the project are the horns, horn cores, skull, atlas, axis, scapula, pelvis, and limb bones. The vertebrae (other than the atlas and axis), carpal bones and sesamoid bones were excluded.

Whenever the material was available, ten known-age male skeletons and ten known-age female skeletons were used. The bone elements of only one side of each skeleton were measured. To supplement these and increase the size of the sample 20 examples of each element (of unknown age and sex) were taken without selection from the randomly collected sample, except to be all from left or right side. In the

archive the origin of each bone from left or right side is recorded.

The dimensions of every bone were recorded in millimetres (mm) using the standard measurements of Driesch (1976). The majority of the measurements were recorded using an osteometric board and digital calipers; at the beginning of the project these were linked to a flexiwriter that produced both hard copy and punched paper tape for reading by the Museum's Varian computer. During the course of the work this Varian computer was exchanged for a PDP computer which could not transcribe paper tape, so the final measurements, those on the older castrate skeletons, were taken on manual calipers. The precise positions of the measurements are shown on the outline drawings of each element.

Despite the need to calibrate the digital calipers and osteometric board every time they were used, and the fact that a number of different people assisted with the measurements, tests for consistency showed that deviations were insignificant. The summaries of the measurements are given in the Appendix, while the complete data base is held as an archive in the British Museum (Natural History), and is available on request.

Criteria for ageing

One of the most important deductions to be made from any assemblage of animal remains from an archaeological site is the age at which the animals had died or had been killed. From this assessment of age the so-called 'slaughter pattern' or 'harvest profile' of the site can be calculated, this being a valuable indication of the economic basis of the site. In order to estimate the age of a jaw or bone at death it is essential to have appropriate comparative material of known age.

Usually the degree of fusion is assessed on prepared skeletal material but it can also be done by radiography. An early attempt by Smith (1956) to establish the times of fusion of the bones of Clun Sheep by X-rays of living animals produced results that differed considerably from those of earlier reports. Whether this was because of the different methods used or whether it was due to a genuinely wide range in the times of fusion has not been determined.

The standard work is Silver (1969) who assembled tables of ages of tooth eruption and epiphysial fusion in the horse, ass, ox, sheep, pig and dog. These give a broad indication of the ages of teeth and limb bones in these animals but much further detailed work needs to be carried out. In 1978 and 1979 two seminars were held in Oxford on the subject of ageing and sexing of animal bones and teeth (Wilson, Grigson & Payne, 1982) but no new detailed information was made available on sheep, one of the difficulties being the lack of distinguishing features for the distinction of sheep from goat jaws.

Although there has been little or no work carried out, during the last 20 years, on the ages at which the teeth of sheep erupt, Payne has made an exhaustive study of the ageing of goat mandibles from the eruption and wear of the teeth (Payne, 1973; Deniz & Payne, 1982) and his system of coding the teeth has been followed in the present work (see Fig. 1). Other systems for ageing the mandibles of goats have been devised by Bullock & Rackham and for sheep/goat by Grant (see Wilson *et al.*, 1982).

Another technique for establishing the age of an animal from its teeth, widely used in the field of wildlife management, is by counting the cementum lines in the roots. In the

archaeological context it has been discussed by Koike & Ohtashi (1987) and by Stallibrass (1982) but not with specific reference to sheep. The annual deposition of cementum should be clearly visible in the Soay sheep which undergo such a regular regime of high and low nutrition. The method has not been used on the specimens in the present study but it is being carried out on a very large sample of mandibles from Soay sheep on Hirta that died after the severe winter of 1986 (T. Clutton-Brock, pers. comm.).

Criteria for sexing

Sexual dimorphism can be seen in the horns and in the skeleton of Soay sheep as in all other sheep. The ram is a considerably larger and heavier animal and the horns are nearly always much larger. Occasionally however, a ram may be found with only a scurr for a horn and this occurs frequently in the ewe. The ewes normally have either no horns or small ones. This dimorphism is reflected in the horn cores, in the skull, and in the size of the bones, as can be seen from the summaries of measurements presented in the Appendix. Further dimorphic characters can be seen in the atlas, the axis, and the pelvis. These characters were first described by Boessneck, Müller & Teichart (1964), Boessneck (1969), Gromova (1953), and Lemppenau (1964), for sheep breeds in general. They have been checked here for both the aged and sexed sample of bones and for the unknown sample. The results are shown in Figures 10-13, 22-24.

Characters of the skeleton that distinguish sheep from goat

Before the 1960's the skeletal remains of sheep and goat (apart from skulls) were not distinguished in reports on animal bones from archaeological sites. This was a grave restriction of the assessment of the economy. Subsequently criteria have been established by which most of the bones of sheep and goats can be distinguished. However these criteria have not been checked against a large collection of bones from a single population of a primitive breed. Our present study sets out to provide this check.

The characters used were first described in detail by Boessneck *et al.* (1964) and Boessneck (1969). Every feature noted by these authors as sheep-like or goat-like was checked against the relevant bones in the Soay skeletons and the feral goats from Holy Island, Arran, Scotland. However, some characters were not clearly described or were too poorly developed in the Soay bones to be defined so these were omitted from the analysis.

RESULTS

Eruption and wear of the teeth

As in all members of the family Bovidae the dental formula of the adult sheep is I: 0/3, C: 0/1, P: 2-4/2-4, M: 3/3 = 32. The lower canine is an incisiform tooth which is placed adjacent and lateral to the third incisor, leaving a long diastema between the incisor arch and the cheek teeth. The formula of the deciduous teeth is di: 0/3, dc: 0/1, dp: 2-4/2-4 = 20.

Deciduous dentition

Payne (1985) has described and illustrated the following morphological features that may be used to distinguish the mandibular milk teeth of lambs from those of kids. In the lower third deciduous premolar (deciduous molar 2 in some terminologies) of the lamb the metaconid is strongly developed and linked to the distal [posterior] part of the tooth by a short ridge running bucco-distally [labial-posterior] while in the kid this ridge connects with a more mesial part of the crown. In addition when viewed from above, the occlusal (biting) surface of this tooth is squarer than it is in the kid where it is more triangular and less robust-looking.

In the lower fourth deciduous premolar (deciduous molar 3 in some terminologies) of the lamb the crown is hypsodont with no prominent basal swelling or interlobar pillar on the buccal [labial] surface.

The cheek teeth of the yearling male, female, and castrate Soays from Hirta all complied with these characters and in no tooth were goat-like or intermediate features seen.

Permanent dentition

INCISORS. An earlier study of the dentition in living Soays, of known age, on Hirta, using portable X-ray equipment, concluded that dental development was slower than in improved breeds of sheep (Benzie & Gill, 1974). It was shown that the Soay took five to six years to reach the 'full-mouthed' stage which is characterized by the eruption of the eight permanent 'incisor' teeth to their full functional height. In improved breeds of mainland sheep in Britain this same stage is reached between three and four years according to Silver (1969) and Ryder (1983, p. 11).

In the present study the dentition of Soays of known age was examined after the death (from natural causes) of each sheep, and these field observations were later verified in the laboratory on the cleaned mandibles. In general the results of Benzie & Gill were confirmed. However, there was considerable variation of the stage of eruption amongst sheep of the same age and sex. This was most noticeable in the three year old males where eruption of the incisors ranged from the rising two-tooth stage to the rising six-tooth stage, with the majority of the animals exhibiting the four-tooth stage as might be predicted from Benzie & Gill's data.

In order to obtain comparative information on eruption of the teeth in castrated sheep the known-age wethers, held at Cambridge, were examined each year from 1978 to 1981. These castrates reached dental maturity at an earlier age. Of three wethers, three-and-a-half years old, two had attained the rising 'full-mouthed' stage, and the third had the complete set of fully-erupted incisor teeth.

All the castrates at Cambridge had reached the 'full-mouthed' stage by four years, a full year in advance of the entire males on Hirta. It would be of interest to know if the hormonal effects of castration cause early eruption of the teeth, especially as it has been claimed that the age of epiphyseal fusion of the bones is, in contrast, delayed by castration. Hatting (1983) reported the early eruption of teeth in castrated, Gotlandic sheep.

CHEEK TEETH (PREMOLARS AND MOLARS). Full dental maturity is reached when all the cheek teeth are erupted and in wear, including the posterior cusp of the lower third molar. In the male and female Soays from Hirta, dental maturity occurs

between the fifth and sixth years although more observations on four-year old sheep are required to establish the range fully. Again the castrates exhibited early eruption of the cheek teeth with full maturity being reached by three and a half years.

The relationship between age and the wear of the teeth in the Soays was investigated using the method devised by Payne (1973, 1987): the wear stage of the occlusal (biting) surface of each cheek tooth is defined by the pattern of the dentine, and represented by a standardized symbol as well as by a numerical code—see Figure 1. Despite the earlier eruption of the teeth in the castrates from Cambridge there are no obvious differences in the degree of wear from that on the teeth of the entire males from Hirta. Nor are there discernable differences in the wear of the teeth between the male and female sheep from Hirta.

Examination of the teeth does, however, reveal that the same state of wear can persist over a wide range of ages. This can be seen best in the lower second molar (Fig. 1d) where stage 9A is found in animals aged from 3 to 9 years. A second example is found in the lower third molar (Fig. 1e) where stage 11G is recorded in animals aged between 6 and 11 years. Finally, the very wide variation should be noted in the wear stages of the lower fourth premolar (one three-year-old with unworn cusps; others with wear up to stage 12S) and the lower third molar (stages 2A to 7G) which are recorded in the group of three-year-old males (Fig. 1b, 1e).

Skeletal pathologies

Pathological conditions are not very numerous but they are found in skeletons of all ages and of both sexes; a number are serious and must have caused considerable distress to the animals. The pathological specimens can be divided into four groups: 1 Deformities of the horn cores; 2 Anomalous teeth, periodontal disease, and abscesses on the jaws; 3 Deformities and lesions on the vertebrae and ribs resulting from trauma; 4 Tumours, abscesses, and exostoses on limb bones.

Horn cores

No pathological condition was observed on the horn cores of male sheep. However the horn cores of female sheep can respond to malnutrition or depletion of essential nutrients during breeding or lactation with a regression in growth, or loss of bone from the horn cores, producing so-called 'thumb-prints', as shown in Plate 1. Severe periodontal disease of the maxilla is also evident in this animal. 'Thumb-prints' can also be seen in both horn cores on the female skull in Plate 2. These indentations in the horn core have received little attention in the literature on osteology or pathology but have been mentioned by Hatting (1975, p. 346). They were present on the left, right, or both horn cores of eleven individuals out of a total of 50 female skulls.

Teeth and jaws

Further evidence for periodontal disease can be seen in the alveolus of the left mandibular ramus in Plate 3 at the junction of M₂ and M₃. This would have caused the animal some discomfort while the loss of all the cheek teeth except P³ in the skull shown in Plate 4 would most likely have led to the sheep's death from starvation. The right mandibular ramus in Plate 5 must be from a sheep that had a bad abscess



Plate 1 Right side of female skull (no. 81.931) to show 'thumb-print' on horn core and periodontal disease of the maxilla.

on its jaw, which probably began with an infection in the root of a tooth. Plate 6 shows the condyle of a mandible with extensive osteoporosis; this sheep, too, is likely to have died from starvation.

Anomalies in the growth of the teeth are illustrated in Plate 7 in which the two incisiform canines of a mandible are displaced and growing inwards, but this probably had little effect on the feeding of the sheep and the wear on the rest of the incisors and cheek teeth is normal.

Vertebrae and ribs

A common pathology in the Soay skeleton has been observed in the centra of the cervical vertebrae of male sheep. In at least one vertebra from each of 14 male skeletons from a total of 23 the posterior, cup-shaped end of the centrum is distorted, flattened, or split, as shown in Plate 8. This condition was never seen in the female. Plate 9 shows a cervical vertebra with a fracture across the anterior end of the centrum and the right transverse process. The assumption to be made from the condition of these vertebrae is that the damage is a result of fighting amongst the heavy-horned rams which batter each other's heads in shock-combat, thereby causing traumatic injury to the neck vertebrae.

The injuries do not extend to the succeeding vertebrae but in 9 out of 19 male skeletons the thoracic vertebrae show extensive ankyloses and exostoses. This is usually seen, as in Plate 10, in the skeletons of male sheep that were more than six years old when they died and the overgrowth of the bone is probably a result of an arthritic condition. In addition a number of ribs show healed fractures which could have resulted from fighting or from falls.

Plate 11 shows a posterior thoracic vertebra in which fusion

has occurred between the transverse process and a rib.

There are few pathologies in the lumbar vertebrae. Plate 12 shows healed breaks on the transverse processes of three of the lumbar vertebrae from the same skeleton as the ankylosed thoracic vertebrae shown in Plate 10. This was an 8 year old male sheep that may have suffered from injuries from a fall or from fighting, as well as developing osteoarthritis in old age.

Limb bones

It is noteworthy that for animals living on steep, rocky terrain there are very few breaks in the limb bones but most of our sample was collected in the relatively sheltered village area. There is one broken metacarpal bone shown in posterior view in Plate 13. The shaft of the bone had broken across diagonally just below the proximal epiphysis and had failed to heal without infection. This caused substantial exostosis and displacement of the two ends of the shaft so that the sheep was probably lame but could have lived a normal life.

The most common pathological condition seen in the Soay limb bones is described in Baker & Brothwell (1980) as 'pen elbow'. These authors claim that, 'shepherds who recognize the condition consider that it is due to trauma to this relatively exposed site when the animals are put through races or pens. Sometimes it is associated with fractures of the olecranon'. The examples in the Soay specimens are typical in having an extra growth of bone or 'lipping' at the lateral edge of the articular surfaces of the humerus and radius, as shown in Plate 14, and exostoses around the joint which reduces its mobility: 37 out of a total of 162 radii show this condition. The articular end of the humerus in Plate 14 also has an extra 'lip' of bone on the medial side.



Plate 2 Female skull (no. 85.946) to show 'thumb-prints' and depletion of the bone of both horn cores.

The Soay sheep on Hirta have never been penned or driven by humans but it is possible that injury to the elbow joint occurs when the sheep crowd together in the cleits.

Plate 15 shows a humerus with a severely deformed distal epiphysis. There is extensive overgrowth of the bone and an eburnation on the medial condyle which is typical of osteoarthritis, as described by Baker & Brothwell (1980).

Radiographic examination of skeletal elements

Although there are some severe pathologies in the bones of the Soays, in general the skeletons appear to be from healthy animals that show little evidence of malnutrition. This agrees with the findings of Benzie & Gill (1974) who made a

radiographic survey of 50 living sheep on Hirta in 1965 and 1966. They concluded that the mineral status of the skeleton of the Soay sheep on the island was good and could compare favourably with mainland sheep grazing on a good hill.

In the present study a series of femora and other limb bones were radiographed in an attempt to identify Harris's lines. These horizontal lines, which reflect a period of retarded growth, can sometimes be seen at the ends of long bones and in the mandible in skeletons of animals or humans that have undergone a period of starvation or stress (Mays, 1985; Baker & Brothwell, 1980). No Harris's lines or evidence of starvation were seen in the radiographs of the Soay bones.

Radiographs of the metapodial bones of the Soays were used by Liora Horwitz to assess the effects of lactation on the thickness of cortical bone relative to the width of the medullary cavity. Horwitz found that the cortical bone of the metacarpals of the female Soays from Hirta was slightly, but significantly, thinner than that of metacarpal bones of female Soays from Babraham, Cambridge, which had been on a uniformly higher plane of nutrition. There was no difference in the cortical thickness of the metacarpal bones of rams from Hirta and Babraham (Horwitz, pers. comm.) However, this thinning of the cortical bone, which results from loss of calcium during lactation, does not appear to have a detrimental effect on the health of the ewes which normally live considerably longer than the rams.

Castrates

The castration of male lambs has been an important part of agricultural practice for thousands of years, with beginnings perhaps as early as the Neolithic period. As every farmer knows, castration causes the lamb, or wether, to grow larger, fatten earlier, and develop a finer fleece. As the Soay sheep on Hirta had been living as a feral population no castration had been carried out in recent times until 1978 when a number of lambs were castrated in order to compare their development and behaviour with that of the rams. These castrates were still alive when the skeletons for the present study were collected, with the exception of two one-year olds which have been included: seven castrates of known age, shown in Table 1, were obtained from the flock of Hirta Soays maintained in Cambridge (see Materials and Methods).

There is some evidence to suggest that castration causes a delay in the time of fusion of the epiphyses of the bones (eg., see Brännäng, 1971; Noddle, 1974), leading to an extension of the period of growth so that castrates are taller animals than the entire males. This theory could not be checked on the castrated Soays because there is no three year old skeleton to compare with the entire males, the bones of which were at the crucial stage of fusion as shown in Figure 2. The bones of the castrate aged three years and five months are all fully fused, indicating that at least in this sheep fusion was not greatly delayed.

Hammond (1940, p. 85) claimed that castration reduces the 'thickness' (ie., the width of the shaft) of the limb bones to that found in the female. The measurements of the Soay castrates (see Appendix) do not show any significant reduction in shaft width over that of other males but it can be seen from Table 2 that their bones are nearly all considerably longer. This increase in length is unlikely to be the result of a higher plane of nutrition in the mainland sheep because, as can be seen from Table 3, the lengths of the limb bones of



Plate 3 Left mandibular ramus (no. 81.290), female, to show periodontal disease.

male sheep from Babraham fall within the same range as those of the male Soays from Hirta (compare Tables with Appendix). It is much more likely that the hormonal changes brought about by removal of the testes leads to a lengthening in the period of growth. Why this should be greatest in the extremities of the skeleton is not known but the measurements show that the facial region of the skull and the lower limb bones are most affected.

Growth, form, and inheritance of the horns and horn cores

Male horns

As in all sheep and goats, the horns of the Soay ram are adapted for use in intraspecific fighting, in which rival males engage in horn-to-horn butting (crashing their horns head-on after running towards each other). Such encounters are often fierce and the horns are therefore strongly developed in the adult, and even as early as one year Soay males have begun to develop short, stout horns (Fig. 3).

By three years of age the male Soay exhibits the typical adult horn conformation; each horn curves outwards and backwards spiralling round the ears, with the tip pointed forward. Although there is a slowing down in the annual incremental growth, male horns continue to increase in length well into old age. This situation may be contrasted with the noticeable plateau in the growth rate that is a feature of horns in the female Soay beyond 5 to 6 years of age (Fig. 3).

Viewed in cross-section, the bases of both the sheath and core in the adult male horn are D-shaped, with the anterior edge more rounded and broader than the tapered, posterior edge (Fig. 4). This broad anterior edge confers strength on the horn; as discussed by Schaffer & Reed (1972, p. 48–51) and Kitchener (1985, p. 191) it is precisely this basal area that receives and must be capable of withstanding the full brunt of the force of impact during butting. Additional strength for the horn comes from the solid construction of the core. Studies of

male and female horn cores by X-rays reveal that in the male the sinus (or internal cavity) is restricted to the basal area whereas in females it occupies up to one half of the total volume and is surrounded by very much thinner walls than in the male (Fig. 5). One of the effects of castration is seen in the extension of the sinus, resulting, in some individuals, in an almost hollow core (Fig. 5).

Compared with the fierce intraspecific fights staged between male sheep, the antagonistic behaviour in male goats is generally less violent and takes the form of rivals clashing their horns, often crossing them at the moment of impact, with the force of impact delivered at a much higher point along the horn's length (see Schaffer & Reed, 1972, Fig. 23, p. 48). As they do not have to withstand such high impact forces, the horns of goats are 'relatively and absolutely more narrow than those of . . . *Ovis*' (ibid, p. 50). Also in goats the horn bases are located further back on the skull and are closer together than in sheep; and irrespective of whether the horns are straight or twisted (depending on breed) the horns of goats are usually more upright than in sheep where part of the horn lies below the dorsal level of the skull.

As in other members of the Caprini (see Kiltie, 1985, p. 316) male Soays show remarkably little variation in horn conformation; and—apart from the occasional incidence of scurred or crumpled (ie. deformed or rudimentary) horned rams—the majority of males within each age group have very similar horn development with only minor differences in size associated with differences in body weights. This conformity is demonstrated by the relatively low coefficients of variation in the lengths of horn sheath of the male yearlings and three year olds on Hirta, in 1979 (Table 4). The 1979 material included a two-year old ram with stunted horns which were short and conical in form, with a circular cross-section at the base. The three-year old group also included one individual male with very reduced sized horns whose presence 'artificially' increased the calculated value of the coefficient of variation in that group (see Table 4). No examples of polled rams were recorded in 1979/80.



Plate 4 Palatal view of skull (no. 81.1719), female, to show loss, during life, of all the cheek teeth except the third premolars, probably a result of extensive periodontal disease of the maxillae.

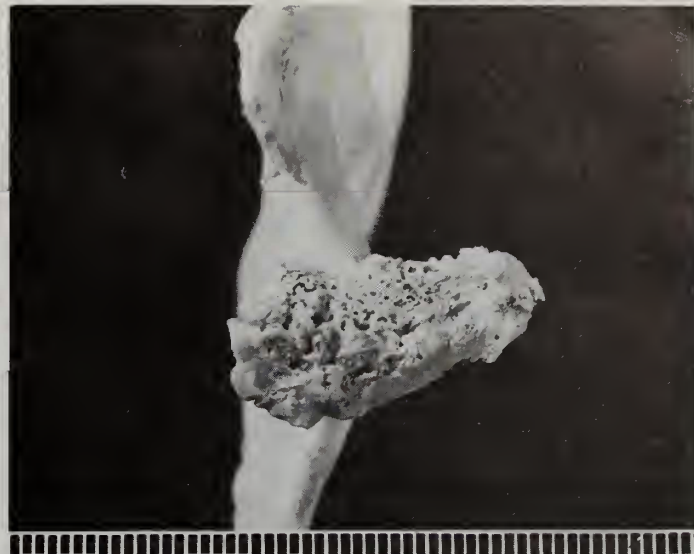


Plate 6 Left condyle of mandible (no. 87.1180) to show extensive osteoporosis. The right condyle is in a similar condition.



Plate 7 Symphyseal region of mandible (no. 87.1179) to show the anomalous position of the incisiform canines which are growing inwards.



Plate 5 Lateral side of right mandibular ramus (no. 78.1883) to show abscess, probably formed at the roots of M_2 and M_3 .



Plate 8 Posterior views of cervical vertebrae (no. 1963.12.17.1), male, to show damage to the centra.



Plate 9 Anterior view of cervical vertebra (no. 78.1633), male, to show the fracture of the centrum and transverse process.



Plate 10 Lateral view of right side of thoracic vertebrae (no. 85.947), male, to show ankyloses.



Plate 11 Dorsal view of 13th thoracic vertebra (no. 1981.1773), male, to show fusion of the transverse process with a rib.



Plate 13 Posterior view of proximal end of metacarpal bone (no. 78.1896) to show exostosis of the bone as a result of a fracture of the shaft.



Plate 12 Dorsal view of lumbar vertebrae (no. 85.947 the same skeleton as the vertebrae in Plate 10) to show healed fractures on the transverse processes.

Female horns

Previous workers have been content to assign the island ewes to the two groups, horned and polled. The present study shows that this is too simple an approach and that the horned and so-called polled conditions are in reality the extremes in a range of conditions, covering a continuum of horn and horn-like structures. Accordingly, it was decided to classify the Soay ewes using the system of Kelley (1951) which recognizes the existence of knobs and scurs as well as the fully horned

condition (ibid, p. 10). Under this scheme it should be noted that the truly hornless state is characterized by concave depressions or smooth (level) surfaces at the horn sites. A measure of the very wide range in forms of horn and scurs in the female Soays on Hirta is the extraordinarily high value (48.2) of the coefficient of variation of horn sheaths of yearling ewes (see Table 4) which fits very well the observations made by Kiltie (1985, p. 315–17). Plots of the length of the horns sheaths from known-age Soay ewes reveal the very different growth pattern compared



Plate 14 Anterior view of left elbow joint (no. 82.706) to show 'pen elbow', a condition in which there is extra growth of bone, or 'lipping' on the medial and lateral edges of the distal epiphysis of the humerus and on the lateral edge of the proximal epiphysis of the radius.

Table 1 Data on the castrates

Reg. no	Killed	Age	Withers height (live) cm	Weight Kg (live)	Metacarpal length* cm
81.1760	May 81	2yr1m	58	24.2	118.9
82.574	Oct 81	3yr5m	66	36.2	130.4
81.1759	May 81	4yr	61	30.2	129.5
84.795	Mar 84	4yr11m	67	36.0	123.2
81.1758	May 81	6yr1m	68	38.0	131.5
84.796	Mar 84	6yr10m	71	39.0	134.6
84.794	Mar 84	8yr11m	67	32.0	127.7
The castrate skeleton from Babraham					
76.1841		6yr4m			124.5

* Measured from the prepared skeleton

with that documented for Soay rams (Fig. 3). Unlike the male, there is no rapid rate of growth in the first three years, but a steady and gradual increase in the growth rate until the 5th or 6th year after which there is only minor annual incremental growth. Throughout life the pace of horn development is much slower than in the male, and the adult female horns in consequence are far less robust and much shorter. The fully developed female horn in the Soay breed is reminiscent of the female goat horn in that both have sharp keel-shaped anterior and posterior edges and are generally flattened medio-laterally; the tip of the horn in the Soay ewe, however, is much more rounded (blunt-ended) than in the goat where it has a sharp, pointed tip.

Effects of castration on the horns

Castration of horned Soay rams within a few days of birth retards the rapid initial growth phase that is characteristic of the entire male (Fig. 3); instead the horns develop very much



Plate 15 Anterior view of distal end of left humerus (no. 78.1893) to show osteoarthritis, exemplified by gross exostosis and eburnation of the medial condyle.

Table 2 Percentage differences between the mean lengths of the bones of the entire male Soays and the castrates.

Element	Castrate longer than male	Entire male longer than castrate
	%	%
Skull	11.28	—
Mandible	12.78	—
Atlas	—	1.07
Axis	—	3.70
Scapula	9.88	—
Humerus	3.20	—
Radius	8.00	—
Ulna		
(length olecranon)	7.50	—
Metacarpal	6.30	—
Innominate	—	.64
Femur	4.70	—
Tibia	8.00	—
Patella	—	2.80
Talus	.11	—
Calcaneum	4.50	—
Metatarsal	9.26	—
Phalanx 1	1.80	—
Phalanx 2	—	.81
Phalanx 3	8.39	—

like those of the female but are somewhat more heavily-built and longer (Figs 4 & 5).

Nordby (1928) recorded a similar retardation in horn development in Rambouillet ram lambs castrated at an early age, and in Merinos, where the males only are horned (the females being either hornless or scurred), castration produced an animal that remained hornless. In field observations made in 1980, on Hirta, it was seen that only those ewes that

BONE AGE (years)	Humerus						Ulna			Radius			Metacarpal		
	prox.			dist.			prox.			dist.			dist.		
sex	M	F	C	M	F	C	M	F	C	M	F	C	M	F	C
new born	u			u			u			u			u		
1	2 u	u	2 u	2 ●	●	2 ●	2 u	3 u	2 u	2 u	2 u	2 u	2 u	3 u	u
2yr 1mth			u			●			u			u			u
3	4 u 3 ○ ○ ●	●		9 ●	●		2 u 4 ● 3 ●			7 u ○ ○ ○	●		2 u ○ 4 ○ 2 ●		
3yr 5mth			●			●			●			●			●
4			●			●			●			●			●
5	●	2 ●	●	●	2 ●	●	●	2 ●	●	●	2 ●	●	●	2 ●	●

KEY

u unfused
○ beginning to fuse
○ part fused
○ almost fused
● fused
M male
F female
C castrate

BONE AGE (years)	Femur						Tibia						Metatarsal			Calcaneum			Phalanx 1			Phalanx 2		
	prox.			dist.			prox.			dist.			dist.			prox.			prox.			prox.		
sex	M	F	C	M	F	C	M	F	C	M	F	C	M	F	C	M	F	C	M	F	C	M	F	C
new born	u			u			u			u			u			u			u			u		
1	2 u	2 u	2 u	2 u	2 u	2 u	2 u	u	2 u	2 u	u	2 u	2 u	3 u	2 u	2 u		2 u	2 u	u	u		u	○
2yr 1mth			u			u		u	u		u	●			u			●		●			●	
3	3 u 4 ○ ●	●		6 u 2 ○ ●	○		7 u ○ ○	○		8 ●	●		2 u 4 ○ ●			2 u ○ 3 ●			7 ●			4 ●		
3yr 5mth			●			●			●			●			●			●		●			●	
4			●			●			●			●			●			●		●			●	
5	●	2 ●	●	●	2 ●	●	●	2 ●	●	●	2 ●	●	●	2 ●	●	●	●	●	●	●	●	●	●	●

Fig. 2a & b The states of fusion of the proximal and distal epiphyses of the limb bones of Soay sheep of known ages up to five years. The number in front of each symbol (see key) indicates the number of individuals in that category.

Table 3 Length measurements (mm) of limb bones from five male skeletons of Soay sheep bred at Babraham, Cambridge.

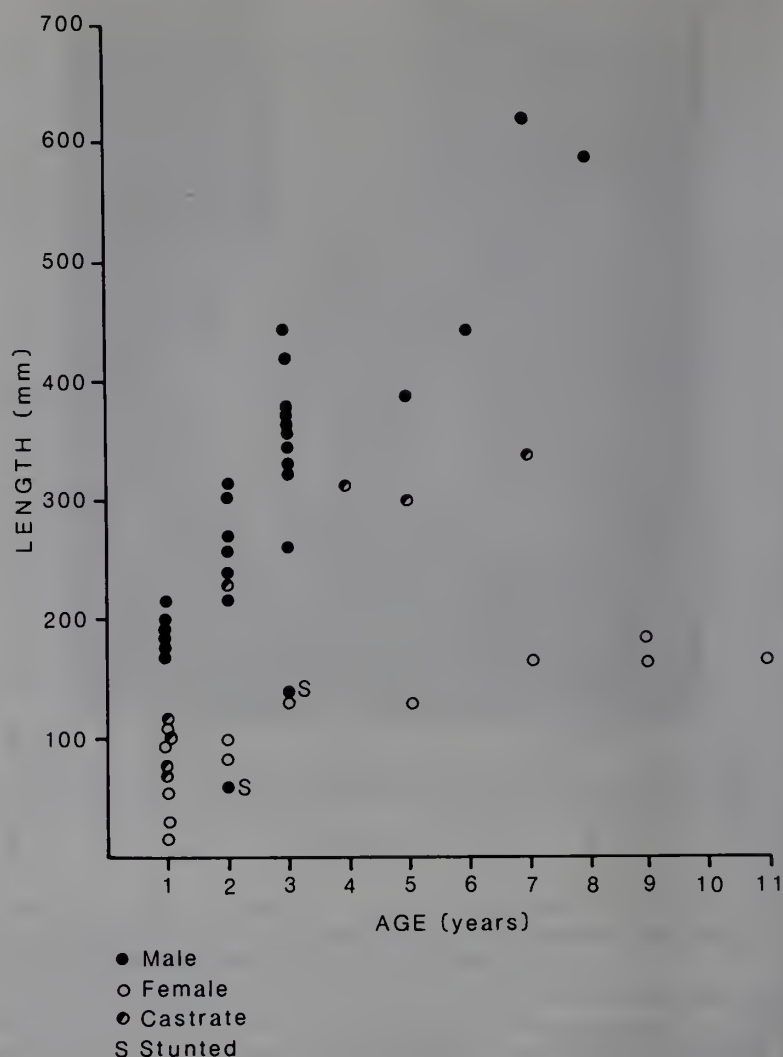
HUMERUS			
	length of bone	max	139.3
		min	129.9
		mean	136.16
		st. dev	3.63
RADIUS			
	length of bone	max	151.6
		min	139.7
		mean	147.36
		st.dev	4.58
METACARPAL			
	length of bone	max	124.4
		min	111.5
		mean	119.04
		st.dev	5.03
FEMUR			
	length of bone	max	170.5
		min	158.6
		mean	165.58
		st.dev	4.97
TIBIA			
	length of bone	max	204.6
		min	189.2
		mean	199.18
		st.dev	6.59
METATARSAL			
	length of bone	max	136.7
		min	123.2
		mean	130.18
		st.dev	5.04

appeared to be hornless produced lambs that grew into polled castrates—conversely, castrated ram lambs of horned ewes all developed horns (Hatting, 1975, 1983 reported similar effects in castrated Gotlandic and Faroese sheep, and see section on horn inheritance, below). It was, however, not possible to ascertain whether those castrates classified as polled were truly hornless or whether some of them had knobs at the horn sites.

The inheritance of horns

The study of horn inheritance in the Soay is difficult because of the considerable variety of horned condition in the ewes. In an earlier study, Doney *et al.* (1974) classified Soay ewes according to the broad categories: horned and 'polled' (including scurred); thereby eliminating the complication of trying to explain the very wide variety of horn and horn-like structures in females. They were able to demonstrate that the phenotypic frequencies followed the Hardy-Weinberg law, based on the assumption that hornedness is controlled by an allele dominant to the one for hornlessness. They acknowledge that horn inheritance in the Soay is probably more complex than this (Doney *et al.*, 1974, p. 98).

The visit to Hirta by P. L. Armitage in August 1980 provided a good opportunity to investigate further this problem. August proved to be an ideal time for such a study as the first phase of horn growth in the lambs was then virtually completed. Moreover, as the lambs had not yet been weaned, it was possible from field observation using binoculars to determine whether or not their dams were horned or polled.

**Fig. 3** Horn sheaths of male, female, and castrated Soay sheep. The length of the horn is plotted against the age of the sheep in years.

It was not possible to distinguish between the truly hornless (clean polled) individuals and those with very small, inconspicuous knobs; and in consequence the data relating to polled sheep include both conditions. Sheep with well developed scurs or stunted/deformed horns were, however, identified and recorded in a separate category from the horned group. The sex of individual lambs was manifest from the colour and arrangement of the ear tags. The data collected are summarised in Tables 5 and 6.

From the collected data the following general 'rules' of horn inheritance in the Soay may be suggested:

1. Irrespective of whether the dam is horned or polled virtually all entire ram lambs are horned and the only example of a scurred male lamb was the progeny of a polled ewe.
2. Polled ewes produce proportionately more polled female lambs than horned.
3. Horned ewes produce proportionately more horned female lambs than polled, and this is true also of those ewes with scurs or stunted horn-like organs.
4. With the exception of a single horned castrate, all of the castrates from polled dams are also polled.
5. With the exception of a single polled female, all of the offspring (irrespective of whether male, female or castrate) of ewes with either scurs or stunted horns are horned.

Apart from the brief analysis published by Doney *et al.* (1974, p. 98) we know of no other study that attempts to explain the

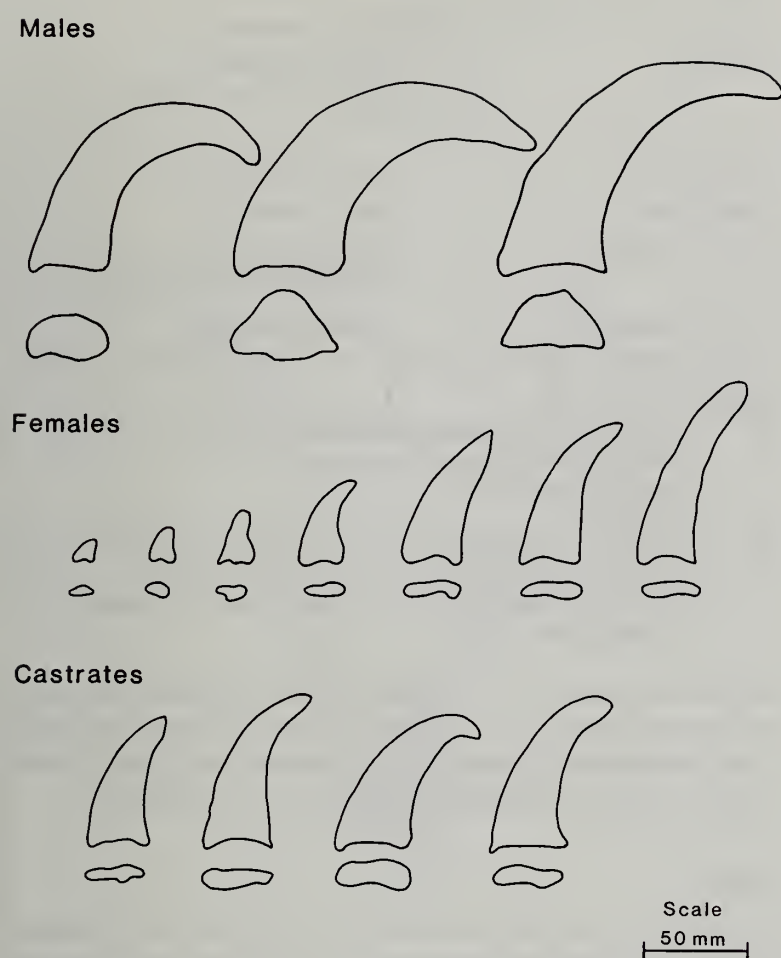


Fig. 4 Horn sheaths of Soay sheep (collected from Hirta in 1979). The lateral profiles and basal shapes have been traced to show the variation in horns of yearling females (top), males (middle), and castrates (bottom).

genetic mechanisms governing horn inheritance in the Soay, despite the appearance of over 200 papers on sheep horns between 1811 and 1981 (see Font *et al.*, 1982). In the absence of any direct investigation of the Soay, the results of work carried out on Merino, Rambouillet and Merino-type sheep are perhaps the most relevant to an understanding of the genetic mechanisms in the Hirta sheep, as in these breeds males are horned and females either polled or have knobs or scurs. A summary of the theories postulated for these breeds is given in Rae (1956): the most plausible theory involved the presence of polygenes that modify the action of the major gene(s) governing the horned and polled conditions. In this way a number of minor (non-allelic) genes (polygenes) influence the expression of the major gene(s) through epistatic and/or hypostatic interactions to produce the observed range of continuous variation 'which has maximal horn-growth and the most concave depressions as its two extremes' (Kelley, 1951).

Although Kelley's theory fits very well the observed evidence for the Soay sheep, he fails to provide any appropriate symbols designating the polygenes; and it is therefore necessary to adopt those used by Ibsen & Cox (1940) and Ibsen (1944) in order to construct a tentative model illustrating the genetic basis of the various conditions recorded in the Soay sheep (see Table 7).

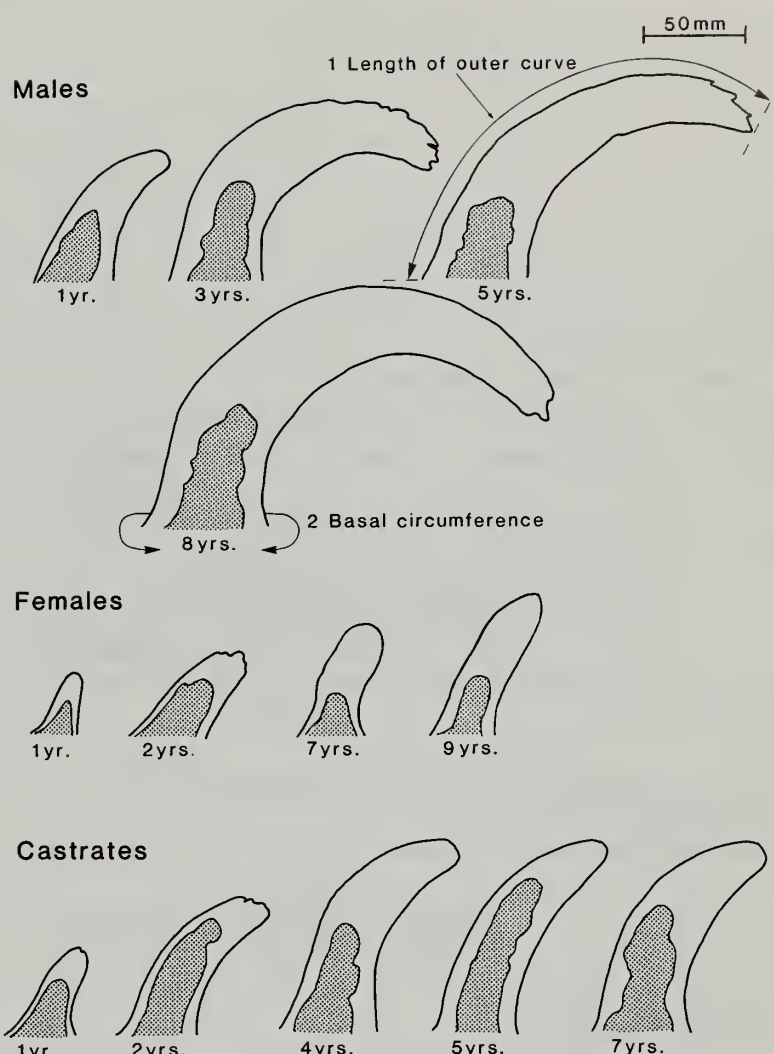


Fig. 5 Tracings of radiographs of the horn cores of male, female, and castrated Soay sheep at different ages to show the location and extent of the sinus (cavity). 1 and 2 measurements (see Appendix).

Description of the skeletal elements and analysis of sheep-like and goat-like characters in the Soay

A system of scoring was devised so that each character was recorded as sheep-like, goat-like, or intermediate between sheep and goat. (A fourth score of anomalous was deleted from the final results as it included so few elements). Every character was visually tested on the Soay skeletons and on the bones of the feral goats from Holy Island, but scores were only analysed from the sheep bones.

The results of the analysis are presented as block diagrams for each character investigated for each element; these readily reveal which characters are diagnostic of sheep, which are closer to the goat pattern, and which are intermediate. The vertical axis in the diagrams gives the numbers of elements in each block and the horizontal axis gives the diagnosis of the blocks. It is important to note that no goat elements are recorded, only those of the Soay sheep. In addition certain characters in the skull, atlas, axis, and pelvis were scored for male-like or female-like and the results are shown in the block diagrams of these elements.

A line drawing of each element is provided to show the points of measurement, signified by numbers, and the characters which are signified by capital letters. The same capital letters are used on the block diagrams and on the legends in which a short description is given of each character.

The mean lengths of the elements in the following descriptions are provided in order to give a general impression of the

Table 4 Length of outer curve (mm) of Soay horn sheaths
(a) Yearlings (1979)—Hirta data only

Sex	N	mean	range	st.dev	Coefficient of variation
male	33	184.4	123–224	25.6	13.9
female	11	70.4	17–109	33.9	48.2
castrate	4	99.5	78–111	–	–

(b) Three year old males—Hirta data only

Sex	N	mean	range	st.dev	Coefficient of variation
male	18	348	135–436	65.4	18.8
	recalculated: excluding the one atypical stumpy horn (length 135)				
	17	360.4	261–436	39.4	10.9

Table 5 Soay sheep, horn inheritance. Phenotypes. Dams with single lambs.

		polled	DAMS scurred/stunted horns	fully horned
OFFSPRING (lamb):				
male	polled	–	–	–
	scurred/ stunted	–	–	–
	fully horned	7	1	6
female	polled	8	–	3
	scurred/ stunted	1	–	–
	fully horned	2	1	3
castrate	polled	6	–	–
	scurred/ stunted	1	–	–
	fully horned	1	–	4

Table 6 Soay sheep, horn inheritance. Phenotypes. Dams with twin lambs

DAMS	OFFSPRING (twin pairs)		
Horned	male horned female horned	female horned female horned	
Scurred/stunted	male horned castrate horned	female horned female horned	female horned female polled
Polled	male horned female polled castrate scurred female polled	male horned castrate polled male horned male scurred	

Table 7 Model of the genetic basis for the presence or absence of horns in the Soay sheep

Phenotype	Suggested genotype* [based on Ibsen (1944)]
horned male	ppHH hmhm srsr
horned female	ppHH HmHm srsr
hornless female	ppHH hmhm srsr or PPHH Hmhm srsr (Srsr)
scurred female	ppHH hmhm Srsr

Key to symbols

H = horned gene (all sheep homozygous = HH)
influenced by following 'factor pairs'

P = polled (epistatic to H)

p = absence of P

Hm = dominant to hm a modifier which causes an otherwise horned female to be hornless

Sr = gene for producing scurs (N.B. gene unable to express itself in the presence of P)

size of the bones. The 'combined mean lengths of the male and female elements' have been calculated from the measurement summaries of 'male aged', 'female aged', and 'male/female not aged' elements presented in the Appendix.

Skull

The skull of the sheep is made up of a great many distinct bones with joints that become completely fused in the adult animal, except for the lower jaw or mandible which always remains a separate movable element (described in the following section).

The skull of a horned and a hornless sheep are shown in the diagrams (Fig. 6 a–d) together with the points of measurement for the dimensions (1–13) which are recorded in the Appendix. The mean condylo-basal length for the sample of male Soay skulls (aged and unaged) is 198.06, for the female skulls (aged and unaged) it is 195.04, and for the castrates it is 220.42. Thus it can be seen that castration increases the length of the skull to a marked extent, a question which was discussed further in the section on castrates (p. 10).

Ageing of the skull can be carried out with considerable accuracy in the sheep and goat by examination of the state of eruption and wear of the cheek teeth (see p. 7).

The sex of the skull of the adult Soay sheep can be determined rather easily from the horn cores as described in the previous section (p. 10). The size of the horn cores has a direct relationship with the degree of robustness of the cranial region of the skull.

Because of the certainty with which the Soay skulls can be sexed the unaged, randomly-collected skulls were recorded as male or female when they were used in the scoring for sheep-like or goat-like characters and it is for this reason that all the skulls in the block diagrams (Fig. 7 A–J) are sexed.

As would be expected, considering the large number of separate elements that make up the skull, there are many characters which distinguish between sheep and goat. Ten of the characters described by Boessneck (1969) are discussed and figured here. The first three of these characters are on the facial region of the skull and the rest are on the cranial region.

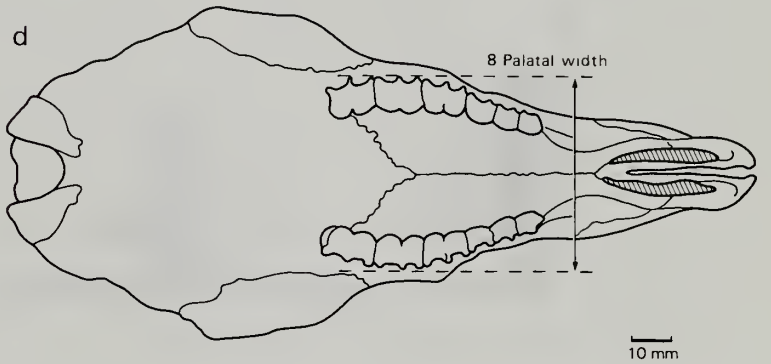
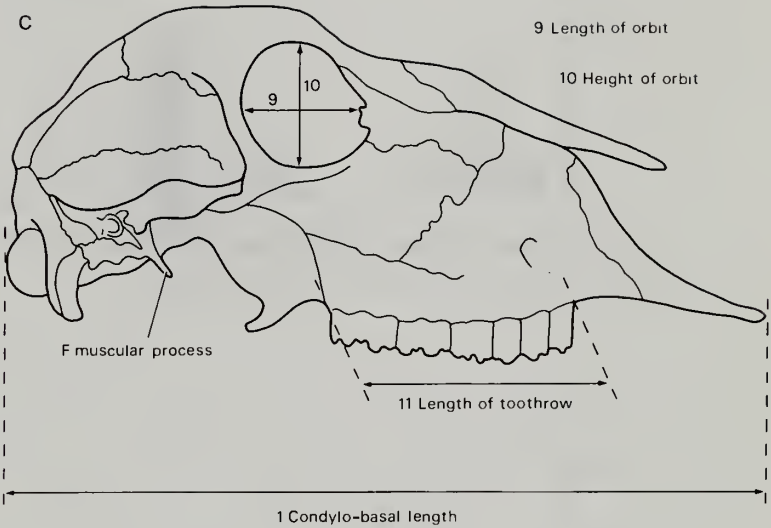
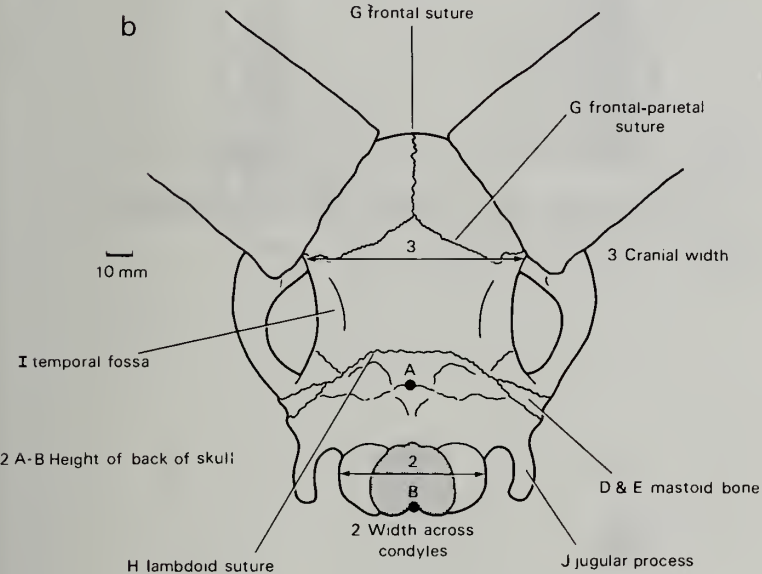
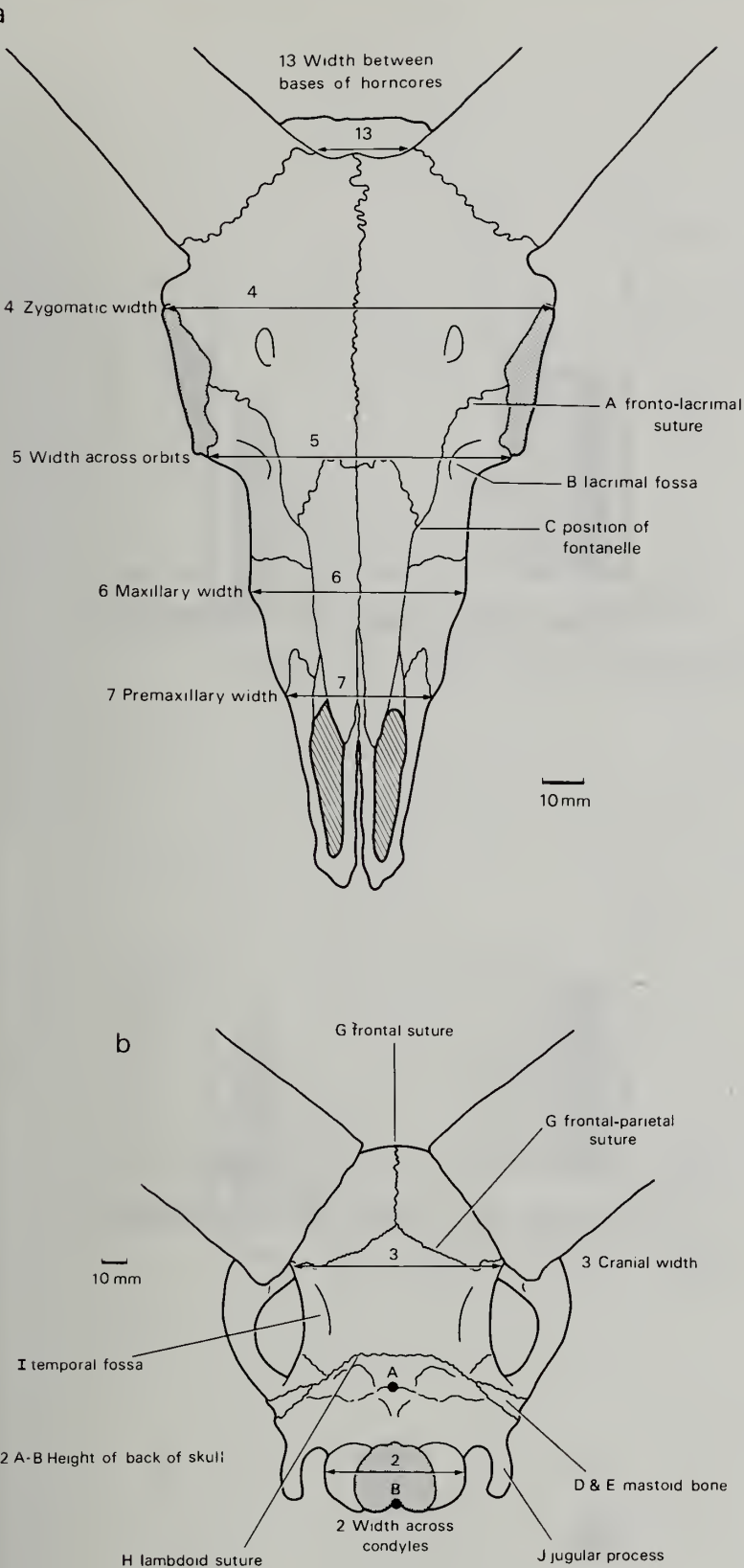


Fig. 6 Skull: **a** dorsal view of skull with horn cores. 4–7 measurements (see Appendix). A–C characters analysed in Figure 7. **b** posterior view of cranium with horn cores. 2–3 measurements (see Appendix). D, E, G, H, I, & J characters analysed in Figure 7. **c** right, lateral view of hornless skull. 1, and 9–11 measurements (see Appendix), F character analysed in Figure 7. **d** palatal view of maxillary (facial) region. 8 measurement (see Appendix).

FACIAL REGION. The suture between the frontal and lacrimal bones (Fig. 6a A) is supposed to be nearly straight and with few serrations in sheep while it is indented and serrated in goats but, as shown in Figure 7 A, this is not a sound discriminant in the Soay skull. Character B (Figs 6a B, 7 B), the presence of a lacrimal fossa in sheep, is the best known distinction and can always be used for separating the facial region of the skull of a sheep from that of a goat. The fossa can be seen as a deep indentation in front of the orbit and it is never present in goat skulls. The third character is also a good discriminant although a male and two female skulls were scored as intermediate. This is the absence of a permanent fontanelle between the nasal and the lacrimal bone in the sheep (Figs 6a C, 7 C).

CRANIAL REGION. Characters D and E (Fig. 6b) are concerned with the mastoid process, the bone which lies between the squamous temporal bone and the paramastoid (jugular) process. In the sheep the mastoid is a small flat bone and not a process; it is wedge-shaped with no lateral projection as is found in the goat (character D) and it has a constriction or concave profile in its mid-line (character E). As can be seen from Figure 7 D and E there were some skulls that were scored as intermediate for these two characters but none was goat-like.

Character F (Fig. 6c) is to be seen on the very delicate muscular process of the tympanic bone which is long and pointed in sheep skulls but short and blunt in goat. Figure 7 F shows that this is a sound character, with few intermediate

Skull

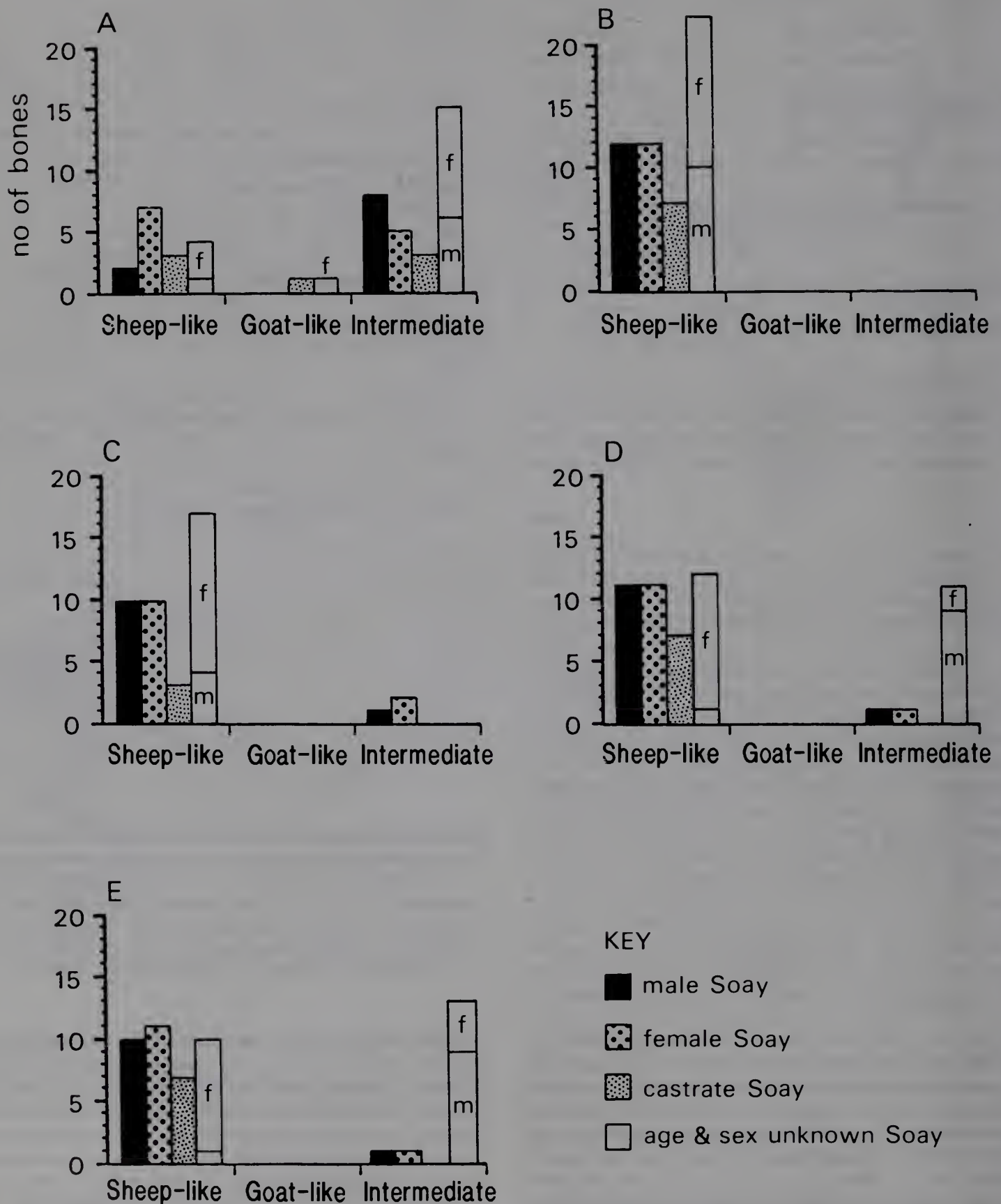
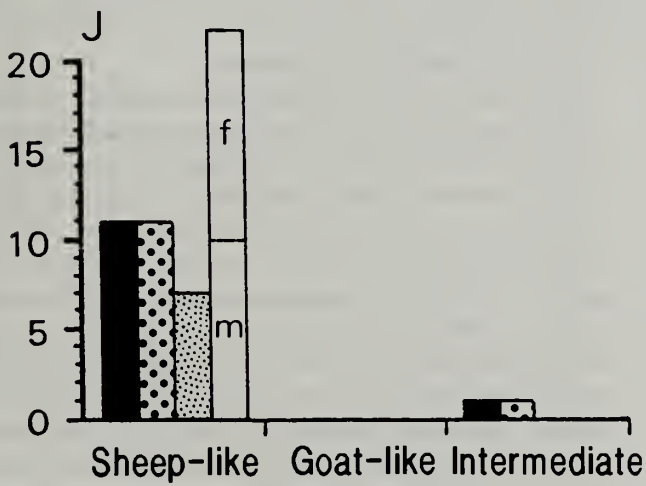
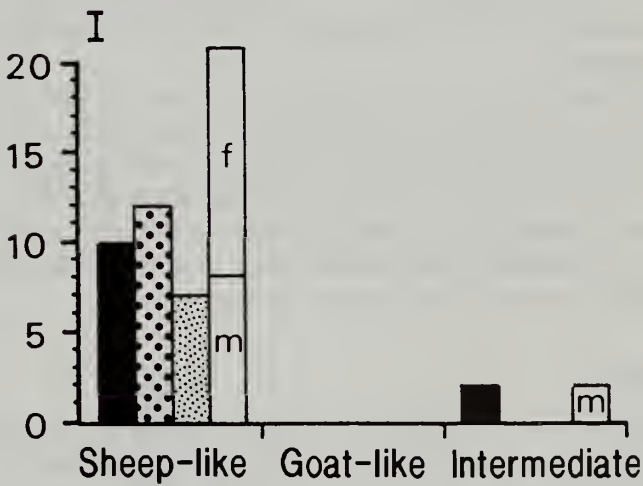
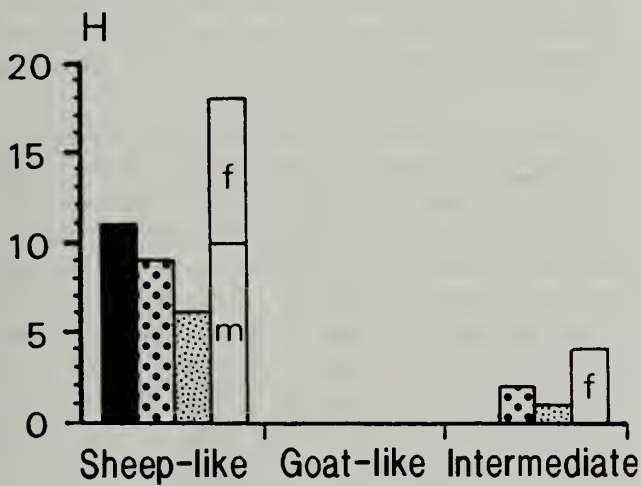
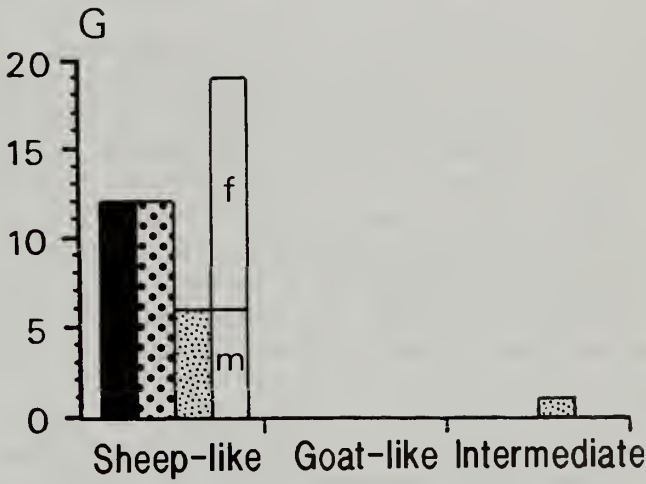
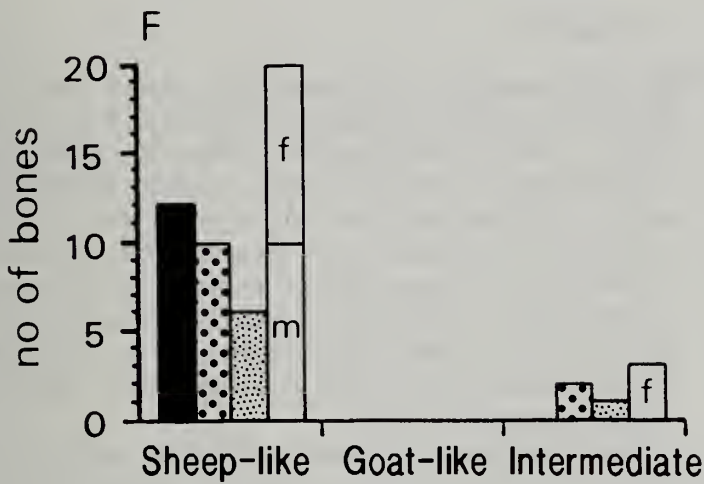


Fig. 7 Skull: analysis of sheep-like and goat-like characters. A fronto-lacrimal suture: sheep—straight with few serrations; goat—indented and serrated. B Lacrimal fossa: sheep—present, goat—absent. C fontanelle between nasal and lacrimal bone: sheep—absent, goat—present. D lateral projection of mastoid process: sheep—absent, goat—present. E shape of mastoid process: sheep—narrow and constricted; goat—broad. F muscular process of tympanic bone: sheep—long and pointed; goat—short and flat. G shape of frontal and fronto-parietal sutures: sheep—involved Y-shape; goat—involved T-shape. H shape of lambdoid suture: sheep—straight; goat—convex. I temporal fossae: sheep—wide apart; goat—closer together. J shape of paramastoid (jugular) process: sheep—long and slender; goat—short and broad.

Skull



KEY

- male Soay
- female Soay
- castrate Soay
- age & sex unknown Soay

specimens, but the process is most likely to be broken off in archaeological material.

The last four characters in the cranial region are well-known diagnostic features: Character G is the shape of the suture between the frontal bones and the parietal bone which is like an inverted Y in the sheep when looked at from the back of the skull, and like an inverted T in the goat (Figs 6b G, 7 G).

Character H is the shape of the lambdoid suture which separates the fused parietal and interparietal bones from the squamous part of the occipital bone (Fig. 6b H). In the sheep this is curved upwards and has a semi-circular or convex profile while in the goat it runs straight across the back of the skull. This is also a sound character in the Soay skulls although there are a few intermediate specimens (Fig. 7 H).

The ninth character (I) is seen in the shape of the temporal fossae which lie on either side of the fused parietal and interparietal bones. These fossae are wide apart in the sheep and close together in the goat (Figs 6b I, 7 I).

The proportional differences in the shape of the cranium in the sheep and goat can be expressed as ratios of measurements as described by Boessneck (1969) who called them the parietal index and the lambdoid index. These indices were calculated for the Soay skulls and they fell within the ranges published by Boessneck but the figures are not recorded here because visual inspection of the bones provides a definitive separation between sheep and goat, so that measurement is unnecessary.

The final character for distinction in the cranium is the shape of the paramastoid (jugular) process which is longer and thinner in sheep than in goats, so that it projects well below the level of the occipital condyles (Figs 6bJ, 7J). This can also be seen to be a sound character, although, as with the muscular process of the tympanic bone, it is seldom preserved in skull fragments from archaeological sites.

Mandible

The lower jaw, or mandible, consists of two elements, the left and right rami which are joined by a symphysis at the anterior, incisor-region. This symphysis hardly ever fuses completely in the sheep, except in very old animals. Each half of the mandible is divided by the angle into a horizontal ramus which holds the incisors and cheek teeth and a vertical ramus which articulates, by means of the condyle, with the zygomatic process of the squamous temporal bone. Anterior to the condyle and divided from it by a notch is the coronoid process which, in the articulated mandible, extends upwards into the temporal fossa and provides attachment for the temporal muscle (Fig. 8).

When separated from the skull it is not possible to establish the sex of the mandible of the Soay. The mean length of the combined male and female mandibles is 149.01, for the castrates it is 167.87, and for the goats it is 180.10 (see Appendix). As with the skulls it can be seen that the length in the castrates is much extended, the extra growth being in the facial region.

The mandible cannot be readily distinguished between sheep and goat and neither of the characters described in Boessneck *et al.* (1964) was found to be sound. The angle of the mandible is supposed to be more oblique in the sheep than it is in the goat but with one intermediate exception all the Soays had the acute angle that is described as goat-like (Figs 8 A, 9 A). The ventral margin of the horizontal ramus

(Fig. 8 B) is described in the same work as more convex in the sheep but it can be seen from Figure 9 B that this character cannot be used, either, as a discriminant. In general it can be asserted that the mandible of the Soay is rather more shallow-boned and straight than is found in many breeds of sheep, perhaps because the teeth are relatively low-crowned.

Vertebrae

The usual number of vertebrae in the spinal column of the sheep is 7 cervical, 13 thoracic, 6 lumbar, 4 sacral, and 18 caudal. However, there may sometimes be 7 lumbar and the caudal vertebrae can vary between 3 and 24 depending on the breed. Only the atlas and axis, the first two of the seven cervical vertebrae found in all mammals, have been included in this study. Characters that discriminate between sheep and goat in the remaining cervical vertebrae, as well as in the thoracic and lumbar vertebrae have been described by Boessneck *et al.* (1964) and in the sacrum by Boessneck & Meyer-Lemppenau (1966).

There is normally a marked sexual dimorphism in the atlas and axis of caprines, those of males with large heavy horns being much more robust than those of females. When attempting to differentiate between these elements in the sheep and goat it is therefore necessary to first separate the males from the females. The works of Boessneck *et al.* (1964) and Boessneck (1969) provide characters for the testing of these discriminants on the atlas and axis of the Soay sheep.

ATLAS. The function of the first cervical vertebra, or atlas, is to support the head and to act as a pivot. It differs from all other vertebrae in lacking a spinous process and a body or centrum. The bone ossifies from four centres and is in three pieces at birth, the ventral arch and two lateral parts. These are usually fully fused in the sheep by 6 months of age.

In the sample of atlas vertebrae from the Soays the mean total length of the male elements is 49.74, for females it is 45.82, and for the castrates it is 50.10. The mean length for the small sample of combined male and female goats is 70.58.

As can be seen from the Appendix the majority of the bones of the castrates are markedly longer than those of the entire males. In contrast, the lengths of the atlas (and the axis) in the castrates are no longer than those of the entire males. Perhaps this is because the size of the vertebra is dependent on the size of the horns and in the castrated male growth of the horns is inhibited so that they only compare in size with those of female sheep.

According to the criteria of Boessneck (1969) the diagnostic parts of the atlas are the modified transverse processes on the posterior ends of the wings (Fig. 10a A, B). These should be short in the sheep and long in the goat. In female sheep the processes should be short and pointed, in male sheep short and blunted, in female goats long and blunted, and in male goats long and pointed. However visual assessment of the length and shape of the transverse processes failed to support any of these discriminants (Fig. 11 A, B) and neither did measurement of the ventral length of the bone against the total length (Fig. 10b). The ratio of these two lengths should give an indication of the relative length of the transverse processes, but there were not found to be any significant differences between the male and female elements, either in the sheep or goat or between the two genera.

A second character that was tested on the atlas vertebrae of the Soays was the shape of the ventral tuberosity (Fig. 10b C).

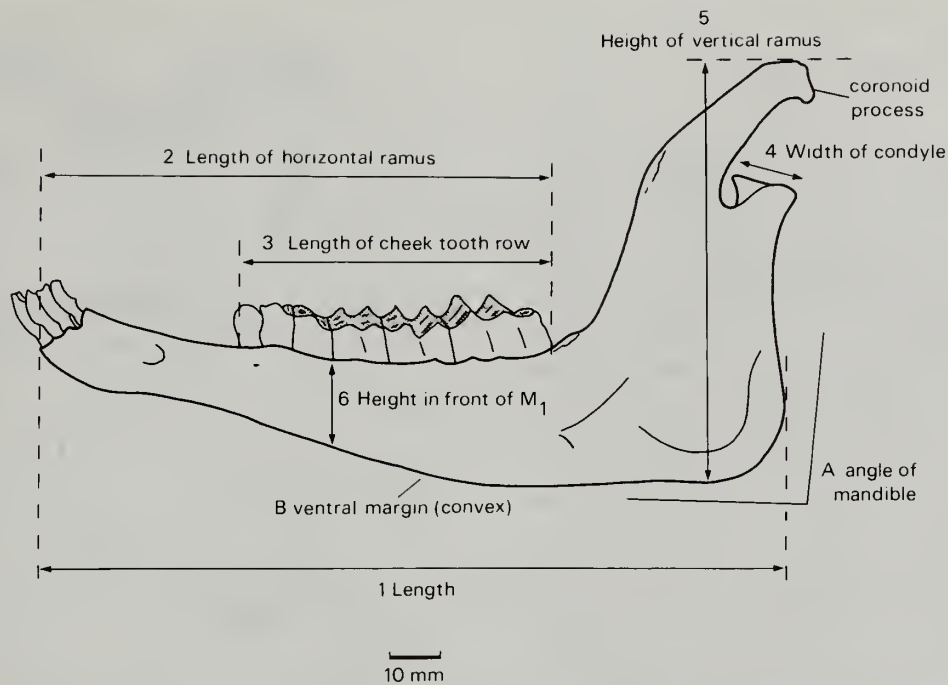


Fig. 8 Mandible: lateral view of left ramus. 1—6 measurements (see Appendix). A, B characters analysed in Figure 9.

Mandible

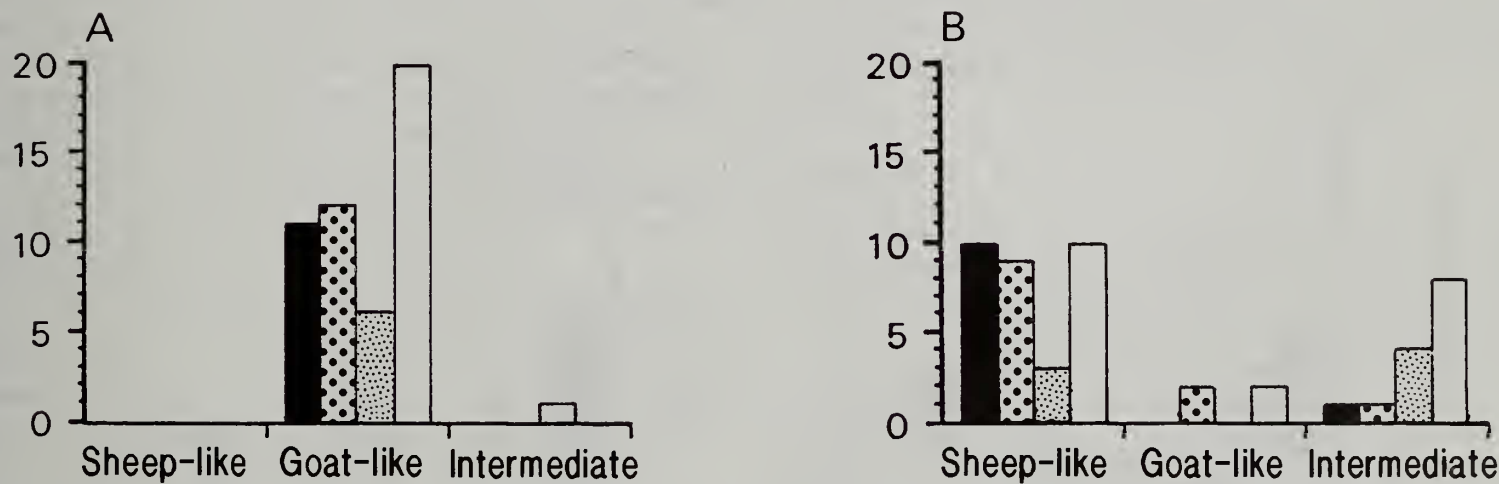


Fig. 9 Mandible: analysis of sheep-like and goat-like characters. A angle between horizontal and vertical ramus: sheep—obtuse; goat—acute. B ventral margin of horizontal ramus: sheep—convex; goat—straight.

This should be broad and ill-defined in the sheep, while in the goat it is narrower, and more ridge-like. As can be seen from Figure 11c, however, this character was not found to be a valid discriminant with the sample of Soay elements.

AXIS. The axis is the longest of the vertebrae and it is characterized by the odontoid process or dens which projects from the anterior end and articulates with the posterior surface of the atlas, resting on the ventral arch. The odontoid process is usually regarded as the displaced body of the atlas and it ossifies from a centre separate from the rest of the axis. The centrum of the axis is usually fully fused by 6 months.

The mean length of the axis vertebrae in the sample of male Soays is 50.41 for the females it is 40.93, for the castrates 53.39, and for the male and female goats 69.87. As with the atlas vertebra it is notable that the mean length for the castrates is only slightly longer than for the male Soays,

showing that this bone does not increase in length to the extent of other bones in the skeleton (Table 2; Appendix).

As described by Boessneck (1969; in which the bone is called the epistropheus) the spinous process of the axis is sexually dimorphic and it is shorter in sheep than it is in goats. The shape of the spinous process (Fig. 12b A, B, C) is dependent on the absence or presence of horns and their size. Assessment of the relative size and shape of the spinous process is shown in Figure 13 A–C. In the sheep the spinous process is short with a rounded or pointed cranial end and a broad rounded caudal end. In the goat the whole process is longer and the ends project further than they do in the sheep. Although, as can be seen from Figure 13 A, B, C, there are some intermediate elements, in general the axis vertebrae of the Soays conform to the sheep pattern. This is supported by measurement of the spinous process; the ratio of the length of the process relative to the length of the body including the

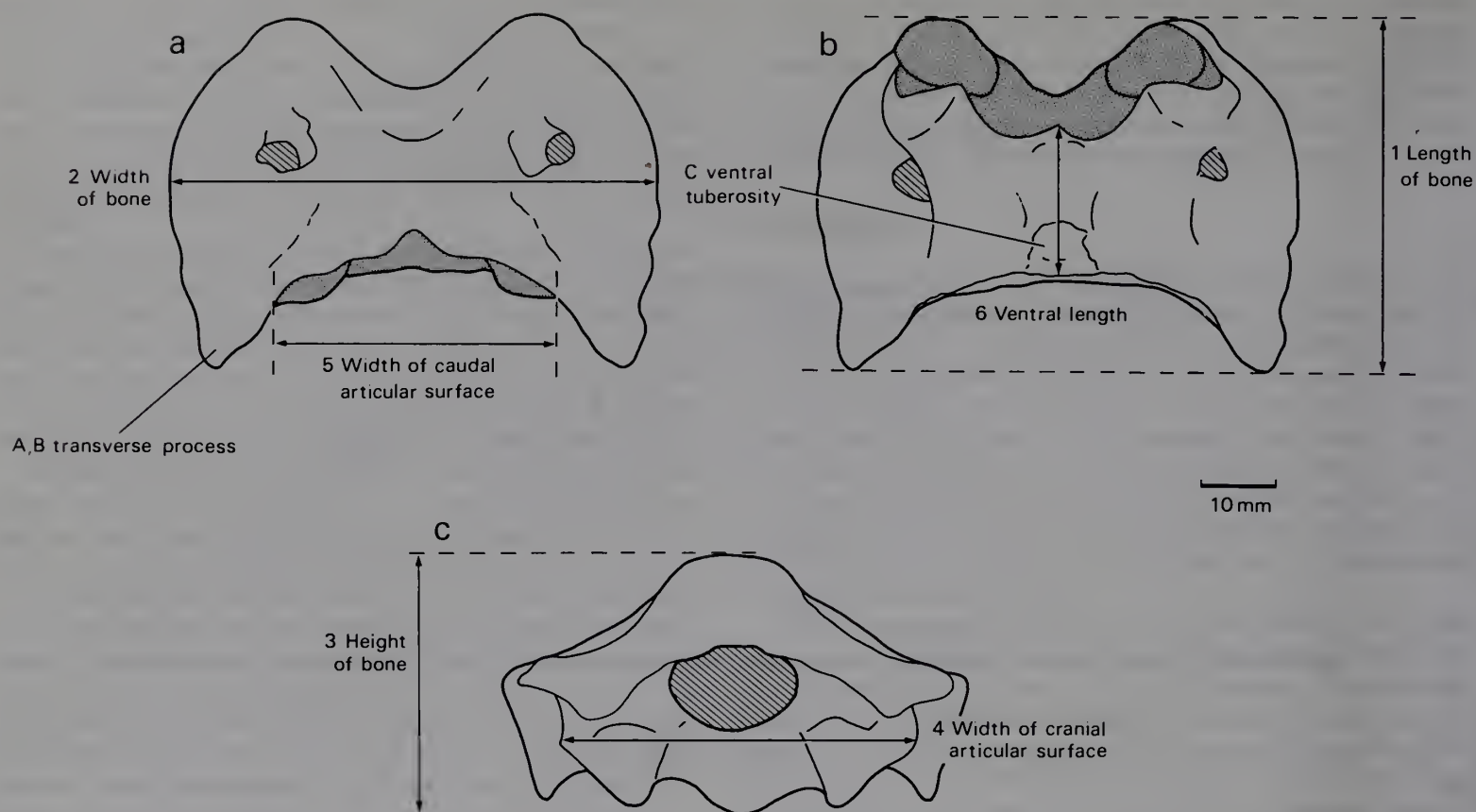


Fig. 10 Atlas: **a** dorsal view. **b** ventral view. **c** cranial view. 1—6 measurements (see Appendix). A, B, C characters analysed in Figure 11.



Fig. 11 Atlas: analysis of male-like & female-like and sheep-like & goat-like characters. A length of transverse process: sheep—short; goat—long. B shape of transverse process: sheep male—short and blunted; sheep female—short and pointed; goat male—long and pointed; goat female—long and blunted. C shape of ventral tuberosity: sheep—broad and ill-defined; goat—narrow and ridge-like.

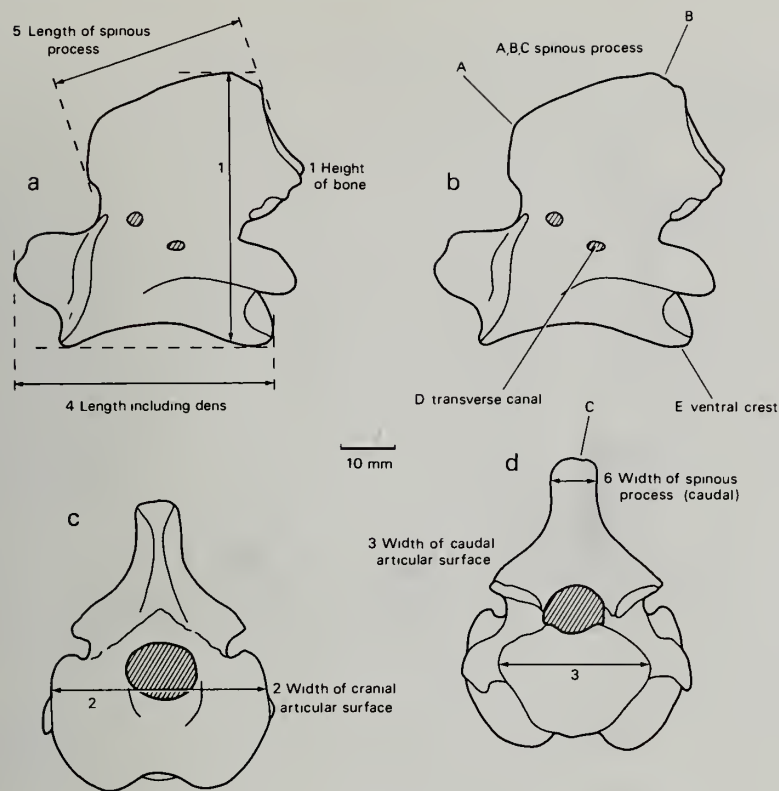


Fig. 12 Axis: **a** and **b** lateral views. **c** cranial view. **d** caudal view. 1–6 measurements (see Appendix). A–E characters analysed in Figure 13.

odontoid process has a maximum of 84% for the Soays and a minimum of 89% for the goat. However the ratio of width of the caudal end to length of the spinous process does not show a significant difference between the Soays and goats for this character, thus agreeing with the assessment in Figure 13C, in which there is a high proportion of intermediates.

Figure 13 D shows that the transverse canal (Fig. 12b D) is present in all the axis vertebrae of the Soays, this being a sheep-like character often absent in the goat.

The development of the ventral crest was used by Boessneck (1969) as a determinant of sex and genus (Fig. 12b E) In old male sheep the ventral crest broadens and flattens at the caudal end while in the male goat it forms a more angular dome. The axis vertebrae of the male Soays conform well to this discriminant as shown in Figure 13 E.

Scapula

The scapula or shoulder blade occupies a movable position on the anterior part of the thorax. In sheep as in all ungulates which have no clavicle the bone is attached to the axial skeleton only by muscles. The scapula is a flat bone with a spine that runs longitudinally along the lateral side for the attachment of the shoulder muscles. The two sides of the spine are slightly hollowed and are known as the supra-spinous and the infra-spinous fossae. The medial side of the bone has no spine and is known as the subscapular fossa.

The shallow cup-shaped distal end of the scapula, known as the glenoid cavity, articulates with the head of the humerus (Fig. 14b). The glenoid cavity is not an epiphysis and ossifies before birth but its anterior margin is bounded by the coracoid process which (according to Silver (1969) where it is called the bicipital tuberosity) fuses in the sheep between six and eight months. In the collection of Soay sheep scapulae

the coracoid process was only unfused in the foetal and newborn scapulae.

The mean height of the combined male and female scapulae is 134.65, that for the castrates is 151.07, and for the goat scapulae it is 177.40.

It is generally agreed that a sound character for distinguishing the scapula of the sheep from the goat is the convex 'bulge' or pecten that develops on the posterior (glenoid) border of the neck in sheep (Fig. 15a B). However it can be seen from Figure 16 B that four scapulae of Soays, two castrates and two males/females were scored as intermediate between sheep and goat for this character. This means that these scapulae had only a slight pecten.

From Figures 15b A, 16 A the concave profile of the anterior (coracoid) margin of the scapula is a good character for distinction with no intermediates. The concavity is dependent on the relative length of the proximal end of the blade which is greater in the sheep than in the goat. The shape of the subscapular fossa (Figs 15b E, 16 E) is also dependent on the width of the blade and shows considerable variation.

In the sheep the spinal tuberosity is according to Boessneck (1969) thick and curved in the sheep but in the Soay scapulae there are a certain number of intermediates for this character (Figs 15a C, 16 C). The angle of the spine as it projects from the blade of the scapula is generally more obtuse on the posterior side, that is it leans further over towards the anterior margin of the scapula, in sheep than in goats. As can be seen from the scores (Figs 15a D, 16 D) there are also a number of intermediates for this character.

Taking all the characters into consideration it is found that the scapula of the Soay, like many other elements, is more goat-like than is usual for the skeletons of improved breeds of sheep.

Humerus

In the living sheep, as in all ruminants, the humerus extends obliquely downwards and backwards. It articulates at its proximal end, in the shoulder joint, with the scapula, and at its distal end, in the elbow joint, with the radius and ulna.

The mean length of the combined male and female humeri is 131.31, that for the castrates is 141.86, and for the goat humeri it is 190.5. The 10 mm difference in length for the mean of the castrates over that for the entire males is notable and is discussed further under the section on castrates (see p. 9, Table 2). The distal end of the humerus is fused in the one year old sheep while the proximal end is still in the process of fusion in the three year old sheep (Fig. 2) which agrees with the data of Silver (1969).

The humerus of the Soay can be distinguished from that of the goat rather easily. In the proximal end the best distinction is the angle of the lateral tuberosity which is broad and projects less far over the sulcus than in the goat where it is high and more pointed (Figs 17a A, 18 A) Below the lateral tuberosity there is the deltoid tuberosity which in the Soay humerus forms a sharp edge that is turned over while in the goat it is more rounded and less marked (Figs 17a B, 18 B). Another distinction was described by Boessneck (1969) in the position of the nutrient foramen on the shaft; this is usually on the posterior side in the sheep and on the lateral side in the goat (Figs 17b C, 18 C). In the distal end of the humerus there are four distinctions; in the sheep there is a thickening, causing a slight protruberance on the lateral border of the trochlear surface which is not present in the goat (Figs 17c D,

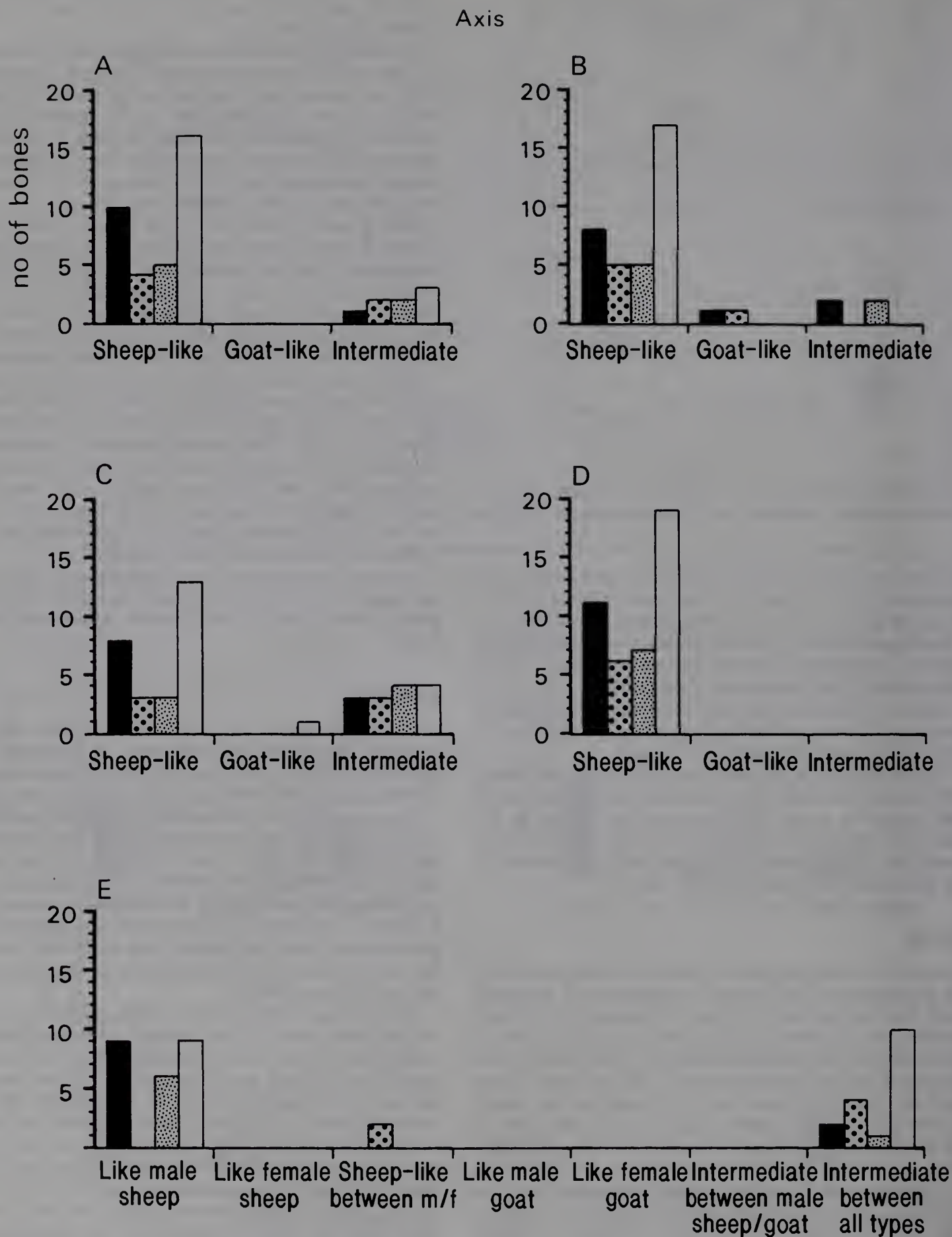


Fig. 13 Axis: analysis of male-like & female-like and sheep-like & goat-like characters. A shape of cranial end of spinous process: sheep—short and rounded or pointed; goat—long and projecting. B shape of caudal end of spinous process: sheep—rounded; goat—angular. C shape of crest of spinous process at caudal end: sheep—rounded; goat—angular. D transverse canal present in sheep; absent in goat. E shape of ventral crest at caudal end: sheep male—broad and blunt dome; goat male—a more angular dome.

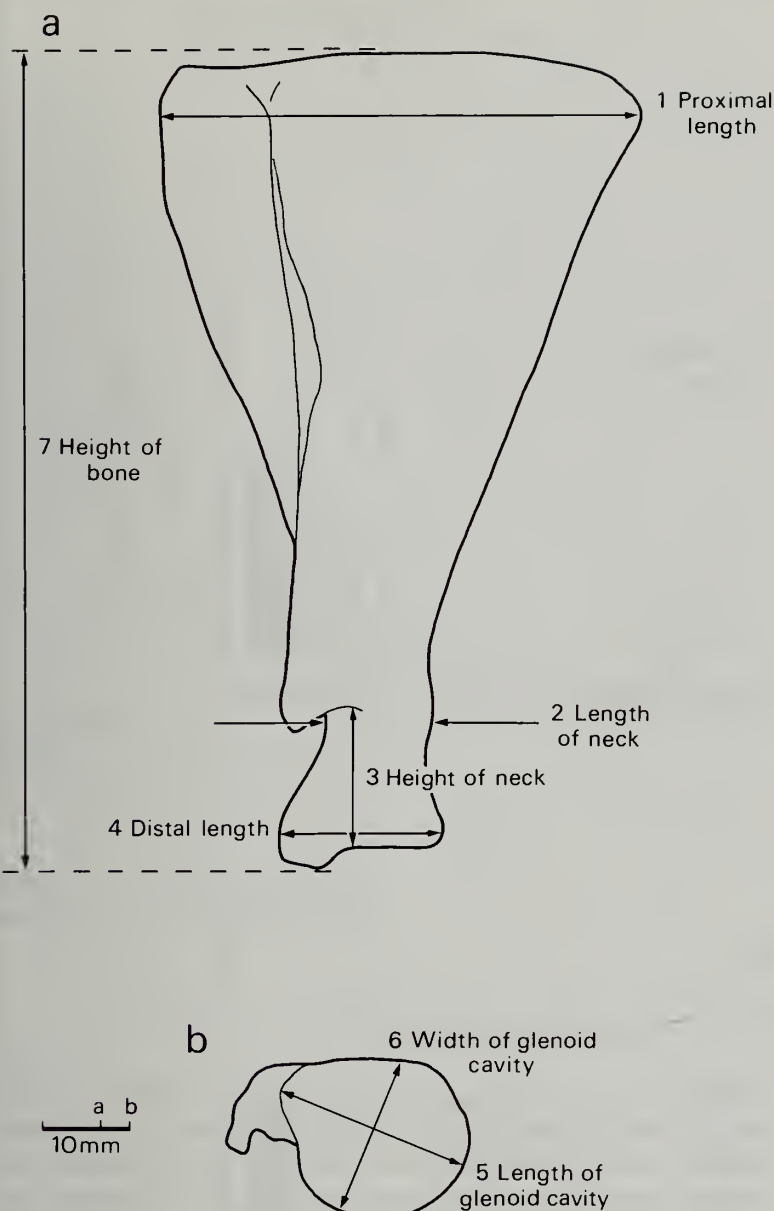


Fig. 14 Left scapula. **a** lateral view. **b** ventral view of glenoid cavity. 1–7 measurements (see Appendix).

18 D); the pit in the lateral epicondyle is surrounded by a marked ridge or crest in the sheep which is not present in the goat (Figs 17c E, 18 E); and the shape of the medial epicondyle is different in the sheep and goat, being rounded and having either a right- or an obtuse-angle in the sheep and being 'cut off obliquely' in the goat (Figs 17c F, 18 F). The fourth distinction is determined by measurement of the distal condyle which is higher in the sheep than in the goat, so that the ratio of height of condyle to distal width of bone is usually more than 46% in the sheep and less than 46% in the goat.

The least consistent of all these characters for distinction of the humerus, in the Soay, is the thickening of the lateral border of the distal trochlear surface (Fig. 17c D). Figure 18 D shows that six of the humeri are scored as goat for this character and eight are intermediate between sheep and goat.

Radius and ulna

These two bones form the part of the forelimb below the elbow joint. Muscles attached to the olecranon process of the ulna and the humerus enable the joint to move in flexion and extension with the action of a hinge. The radius is a larger bone than the ulna and the two shafts may be fused in the

inter-osseous space at their proximal ends. The distal end of the radius articulates with the carpal bones which form the first section of the manus. In ungulates this joint is commonly known as the 'knee'. The carpal bones have not been included in this analysis of the skeletal elements of the Soay.

The mean length of the combined male and female radii is 139.05, for the castrates it is 153.83, and for the goats it is 185.40. The length of the ulna was not measured because of its curved profile; however, the mean length of the olecranon process in the combined male and female sample is 36.72, in the castrates, 41.64, and in the goats, 52.64.

Silver (1969) gives an age of 6–8 months for the fusion of the proximal epiphysis of the radius. In the Soay radii the proximal epiphysis is unfused in the newborn lambs and fully fused in the one year olds. As can be seen from Figure 2 the distal epiphysis of the female radius of the three year olds is fused while in the nine male, three year old radii the distal epiphyses are unfused in seven, beginning to fuse in one, and part fused in one. There are eight male ulnae, two with unfused olecranon processes, four part fused and three fused. These fusion times for the distal end of the radius and the olecranon of the ulna are later than those recorded by Silver (1969) which are three years for the distal radius and two and a half years for the olecranon.

The most distinctive feature of the sheep radius is the formation of a 'ledge' on the lateral border of the proximal epiphysis which is not found in goats (Figs 19b B, 21 B). An easy distinction is generally assumed to be the lack of fusion between the proximal articular surfaces of the radius and ulna, but in the Soay specimens a number are fused or part fused (Figs 20a A, 21 A). Distinctions in the distal end of the radius are difficult to describe; however, a long narrow facet (the radiale facet of Boessneck, 1969) for articulation with the scaphoid seems to be typical of the sheep (Figs 19c C, 21 C).

The ulna is not very easy to differentiate between sheep and goat. According to Boessneck (1969) the medial edge of the olecranon process should be slightly convex in sheep while in the goat it is almost straight, but the scores for this character in the Soays show a high proportion of intermediates (Figs 20b D, 21 D).

Measurement of the olecranon provides two indices that can discriminate sheep from goat. The olecranon process is usually longer in goats so that if the length is divided by the depth (Fig. 20a) an index of less than 160% will indicate that the bone is sheep, while the proximal end of the bone is thicker in goats so that if the index of width divided by depth is less than 46% (Fig. 20c) then again the bone is probably sheep, but for both characters a higher index cannot be taken as definitive of goat as some of the Soay ulnae have long and thick olecranons.

Pelvis

Apart from the skull the pelvis is the most complicated bone in the skeleton. It links the vertebral column and tail with the hind limbs and, in the female, it provides a channel through which the foetus is born. Like the scapula the pelvis is generally regarded as part of the appendicular skeleton. It is joined to the axial skeleton at the sacrum by the sacro-iliac joint, which has only a very limited degree of movement, its stability being secured by the very powerful sacro-iliac ligaments.

In the adult sheep, as in all mammals, the pelvis, or pelvic girdle, consists of two bones known as the left and right

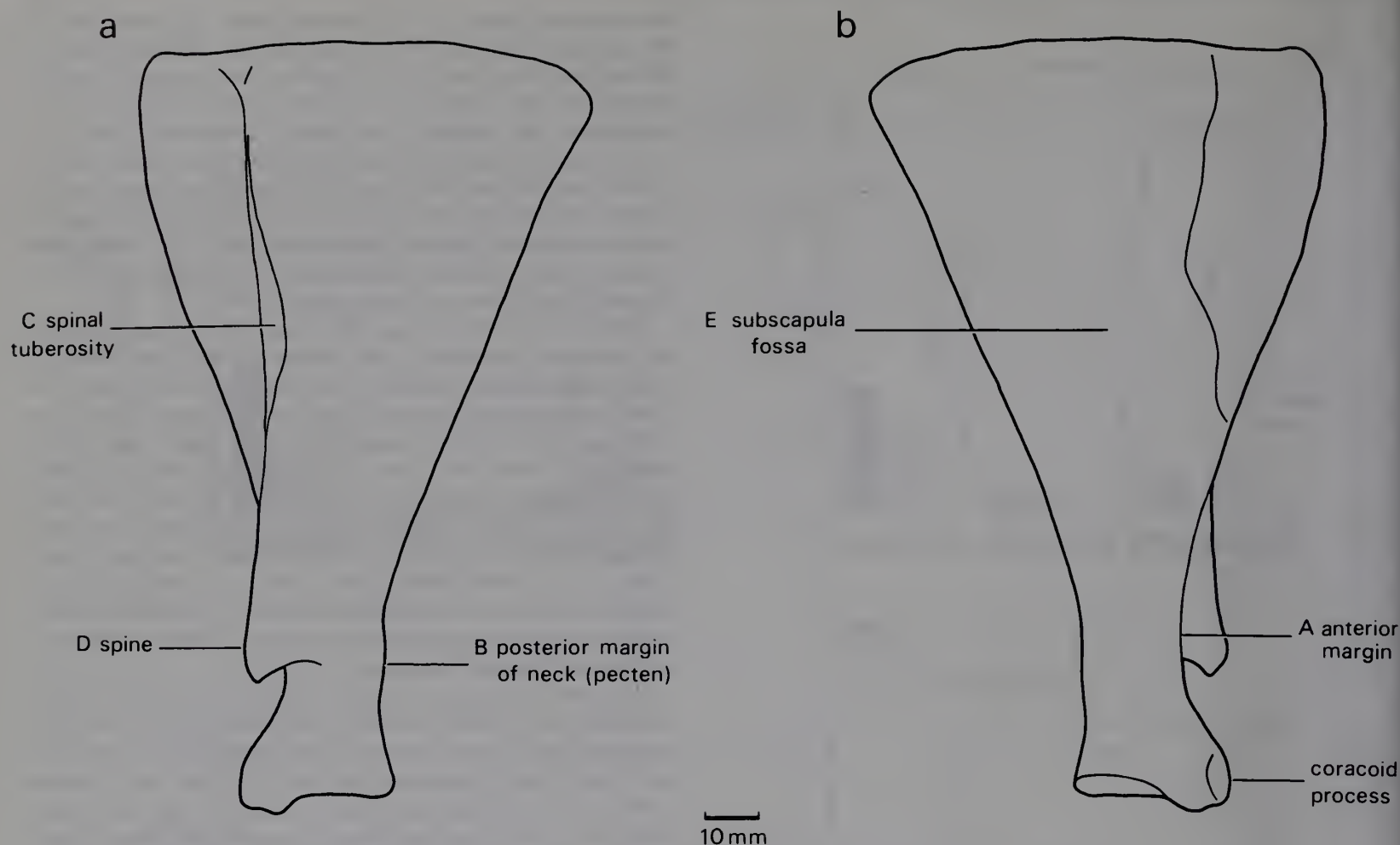


Fig. 15 Left scapula: a lateral view. b medial view. A–E characters analysed in Figure 16.

innominate bones or *os coxae*. These two bones are joined ventrally in the mid-line of the body at the pubic symphysis. In the foetus and in young mammals each innominate bone consists of three separate elements, the ilium, ischium, and pubis which fuse as the animal grows until the symphyses are completely invisible to the naked eye. In the sheep this usually occurs by the age of three and a half years (Silver, 1969). However, because of its complicated structure the pelvis is not a very useful bone for the assessment of age and it has not been included in Figure 2.

In the sample of pelvic bones of the Soays the mean total length of the male innominate bones is 185.69, for the females it is 175.95, and for the castrates 184.5. The mean width of the pelvis across the acetabula is 95.02 in the males, 93.87 in the females, and 97.75 in the castrates (Fig. 22; Appendix). These figures are of interest in showing that in overall dimensions the female pelvis is wider for its length than that of the male and the castrate; greater width being required in the female for the passage of the foetus at birth.

Boessneck (1969) claimed that the ilium in sheep and goats is longer in the female than in the male but measurement of this element in the Soays does not support this (Fig. 22; Appendix). However, three qualitative characters described by Boessneck as being sexually dimorphic do discriminate satisfactorily between the male and female Soay innominates. The first character is the shape of the iliac wing (Fig. 23 A) which is blunt and usually rounded in male sheep and goats, while it is extended and pointed in female sheep and goats. The second character is to be seen in the pubic bone (Fig. 23 B): in male sheep and goats the pecten which forms on the robust ventral border of the bone is rounded and indistinct,

while in female sheep and goats this border is slender and the pecten forms a sharp ridge. The third character is seen in the shape of the ilio-pectineal eminence (Fig. 23 C). This is pad-shaped in male sheep and goats while it is sharp-edged, or even developed as a point, in females. The block diagrams shown in Figure 24 A, B, C show that these characters do separate male and female innominate bones although there are a few intermediate specimens. The innominate bones of the castrates, on the other hand, are anomalous and fall into all three categories of male, female, or intermediate.

It is not very easy to distinguish between the innominate bones of sheep and goats but there is one feature on which they can be separated. In goats the anterior end of the obturator foramen is extended forwards into a small semi-circular notch which leads into the dorsal side of the acetabulum (Fig. 23 D). This obturator notch is not present on the innominate bones of the Soays although it appears to be very slightly developed in one element and so was scored as intermediate (Fig. 24 D).

A second, generic character that can be used to separate female sheep from goats is the development of a muscle ridge on the ventral surface of the body of the ileum (Fig. 23 E) but this is not present in male sheep or goats. In female sheep the ridge is short and narrow, giving a distinct demarcation to the pit for the rectus femoris muscle, while in female goats this area is longer and more strongly ridged. Figure 24 E shows that there is a good separation for this character in the female innominates which all fall into the 'female sheep-like' character. The male innominates also conformed in having no muscle ridge but five of the seven castrates had developed a ridge as in the females.

Scapula

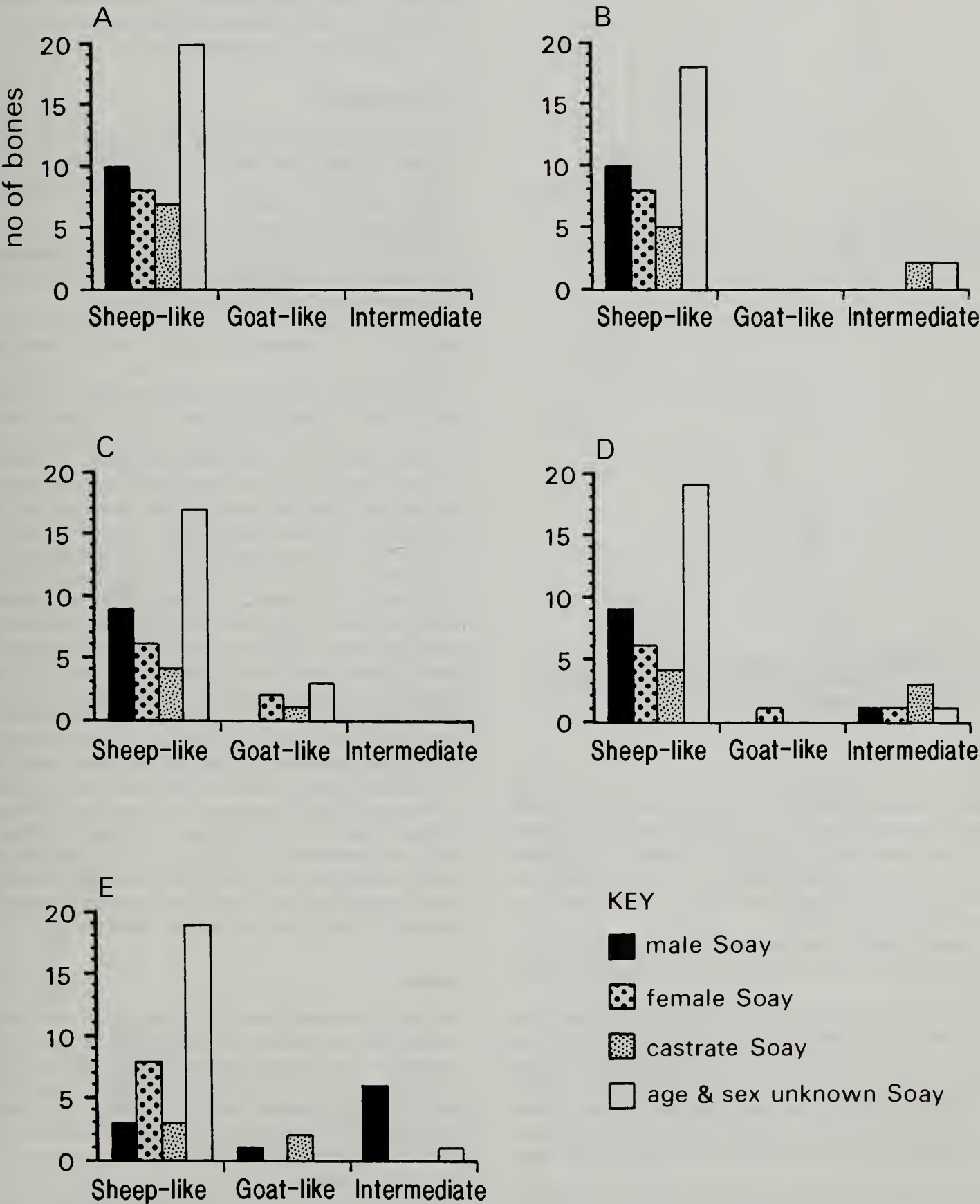


Fig. 16 Scapula: analysis of sheep-like & goat-like characters. A shape of anterior margin: sheep—strongly concave; goat—less concave. B pecten on posterior margin: sheep—present; goat—absent. C shape of spinal tuberosity: sheep—thick and curved; goat—sharp and runs in a straight line. D angle of spine: sheep—obtuse; goat—acute. E shape of subscapular fossa: sheep—broad and flat; goat—narrow and restricted by a distinct eminence towards the cervical border.

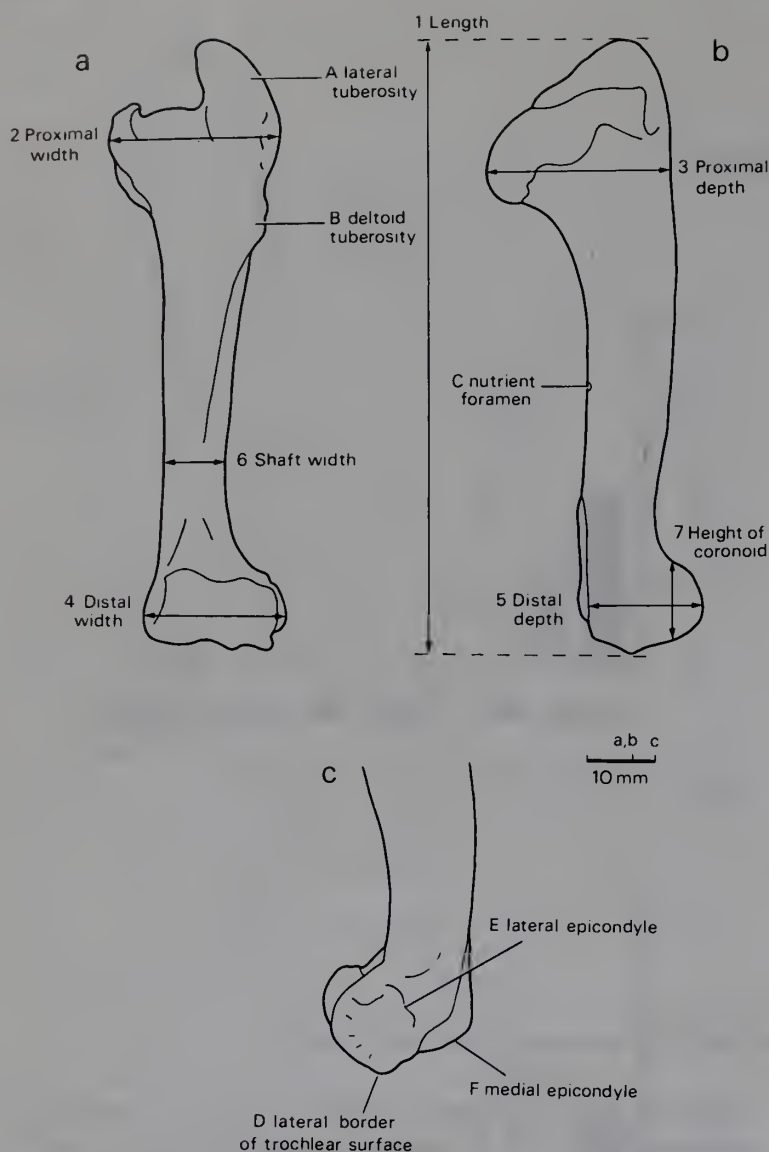


Fig. 17 Left humerus: a anterior view. b medial view. c lateral view of distal end. 1–7 measurements (see Appendix). A–F characters analysed in Figure 18.

Femur

The femur is an equivalent bone to the humerus of the forelimb; it connects the hip joint at its proximal end with the stifle joint at its distal end. The stifle joint, which is equivalent to the human knee, unites the end of the femur, the proximal end of the tibia, and the patella. The femur is the most massive bone in the skeleton and it stretches downwards and forwards in the living animal.

The mean length of the the combined male and female femora is 161.34, for the castrates it is 174.65 and for goats it is 202.70.

Silver (1969) gives 2½–3 years for the age of fusion of the proximal end of the femur (head and greater trochanter) and 3–3½ years for the distal epiphysis. In the femora of the Soay sheep (Fig. 2) only one proximal and one distal end are fused from the three year old male sheep, while the female femur has the proximal end fused and the distal end part fused which agrees with Silver's later date for the fusion of the distal end.

The proximal end of the Soay femur is relatively easy to distinguish from that of the goat as shown by the results of the character analysis given in Figure 27 A–C. In the sheep the head forms a continuum with the 'saddle' at the proximal end; in the goat the head is shaped like a ball and is cut off from

the saddle (Fig. 25b A). The greater trochanter at the lateral side of the bone forms a separate epiphysis from the head and is flat across its top in the sheep, but this is a slightly less reliable character with some bones showing an intermediate state (Fig. 25d B). The square edge to this trochanter is also a character that is a nearly foolproof distinction (Fig. 25d C). There is only one distinguishing character at the distal end of the femur which is the absence of a synovial pit in the sheep (Figs 25b D, 27 D). However the frequency of absence of this pit in the goat has not been assessed.

Tibia and fibula

These bones are the equivalents of the radius and ulna of the forelimb although in the sheep, the fibula is extremely reduced. The tibia connects the stifle, a hinge joint like the elbow, with the hock joint.

In the sheep and goat the fibula is represented by a small projection on the lateral side of the proximal epiphysis of the tibia and by the lateral malleolus which articulates with the distal end of the tibia; there is no fibula shaft.

The mean length of the combined male and female tibiae is 188.55, for the castrates it is 209.63, and for the goat it is 246.30.

According to Silver (1969) the proximal end of the tibia should fuse between 3–3½ years and the distal end rather earlier at 1½–2 years. In the Soays the fusion times appear to be rather behind this, as shown in Figure 2. None of the proximal ends is fused at 3 years and one of the distal ends is still only part fused at 3 years. On the other hand the castrate has proximal and distal ends fused at 3 years 4 months.

The tibia is a bone that is difficult to distinguish between sheep and goat. The proximal end relies on the conformation of the nutrient foramina. In the goat there is usually one circular foramen encircled by a wider pit. In the sheep there is no pit and there can be either one or several foramina that are placed flat on the surface of the bone (Fig. 26b A). The shape and position of these foramina are quantified in Figure 27 A, and it can be seen that there are only two elements in which the foramina do not conform to the typical arrangement.

Following Boessneck (1969) no characters were analysed for the distal end of the tibia. This has been done, however, by Prummel (1986) who gives a description of three distinguishing characters. One of these, the trapezoid shape of the distal end, can be seen in Figure 26c. In the goat this profile is nearly rectangular. In general the distal end of the tibia is rather variable in shape and is not considered to be a useful element for the distinction of sheep from goat.

Patella

This is a sesamoid bone that articulates with the distal trochlea of the femur; its function is to give increased leverage to the femoral muscles in the stifle joint. It is of interest that even this bone becomes rather longer in a sheep that has been castrated than in an entire ram. The mean length of the combined male and female patellae is 26.98, while for the castrate it is 28.12, and for the goat it is 37.53 (Fig. 28a, b; Appendix).

The bone has no epiphyses and so it cannot be aged. The patella was not included in the sheep and goat distinctions described by Boessneck (1969) but it was mentioned in the earlier work of Boessneck *et al.* (1964). On the antero-proximal face of the bone there is usually a sulcus

Humerus

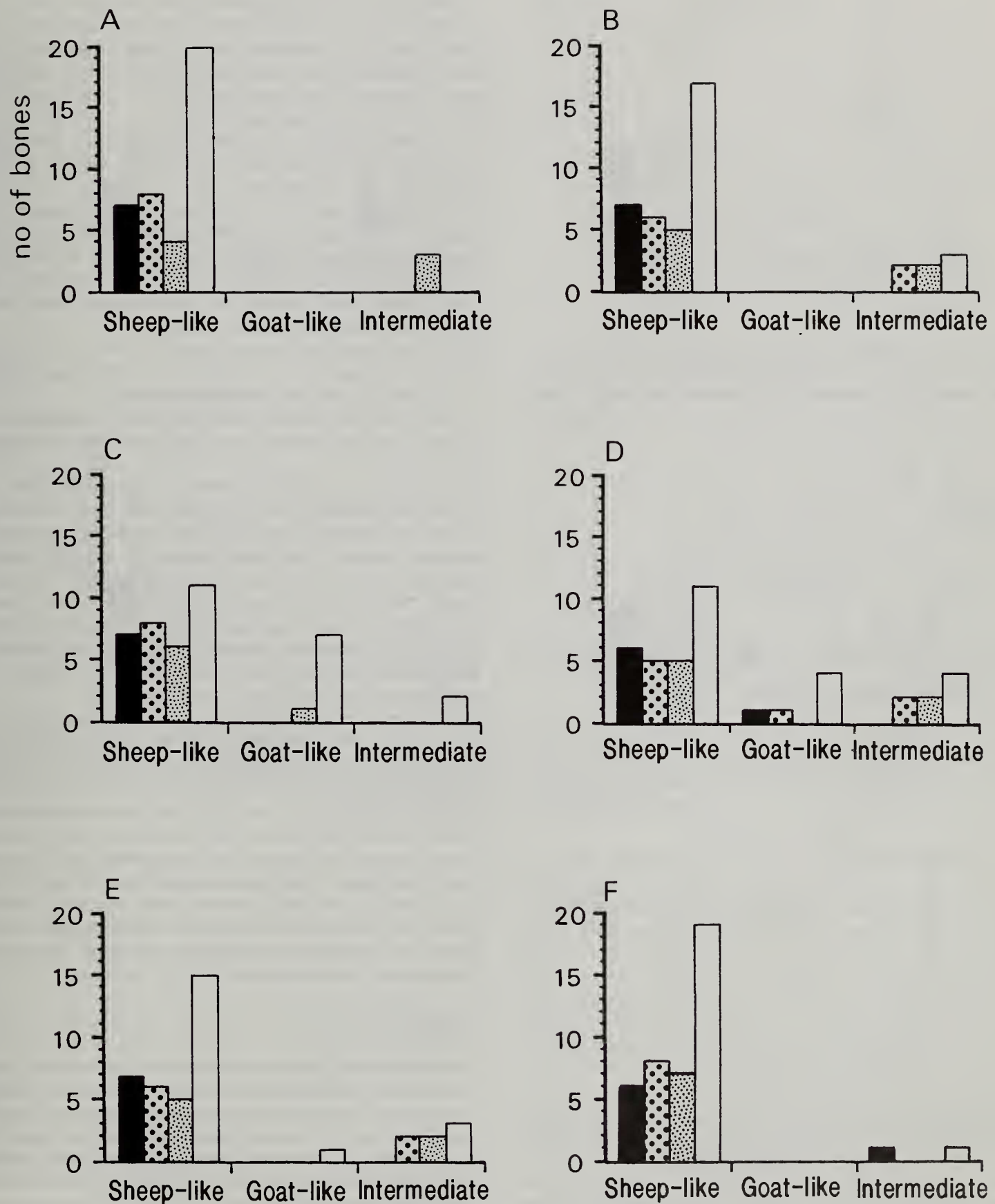


Fig. 18 Humerus: analysis of sheep-like & goat-like characters. A shape of lateral tuberosity of proximal articular surface: sheep—broad and low; goat—high and narrow. B shape of ridge below deltoid tuberosity: sheep—sharp and turned over; goat—straight and blunt, becoming indistinct distally. C position of nutrient foramen: sheep—on posterior side of shaft; goat—towards lateral side of shaft. D shape of distal trochlear surface: sheep—thickening on lateral side; goat—absent or slight. E shape of lateral epicondyle (distal end): sheep—crest on edge around pit; goat—crest absent. F shape of medial epicondyle: sheep—ends in an angle between acute and obtuse; goat—angle is cut off obliquely.

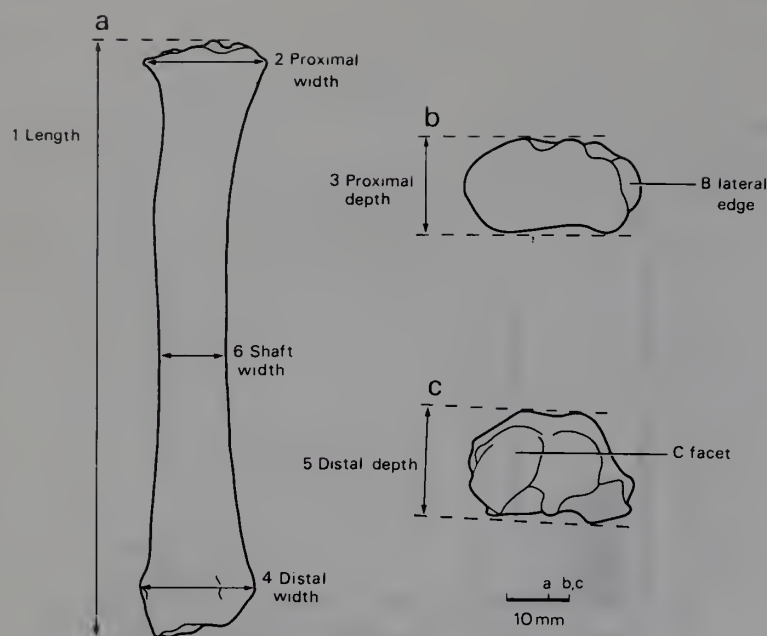


Fig. 19 Left radius: **a** anterior view. **b** dorsal view of proximal articular surface. **c** ventral view of distal articular surface. 1–6 measurements (see Appendix). B, C characters analysed in Figure 21.

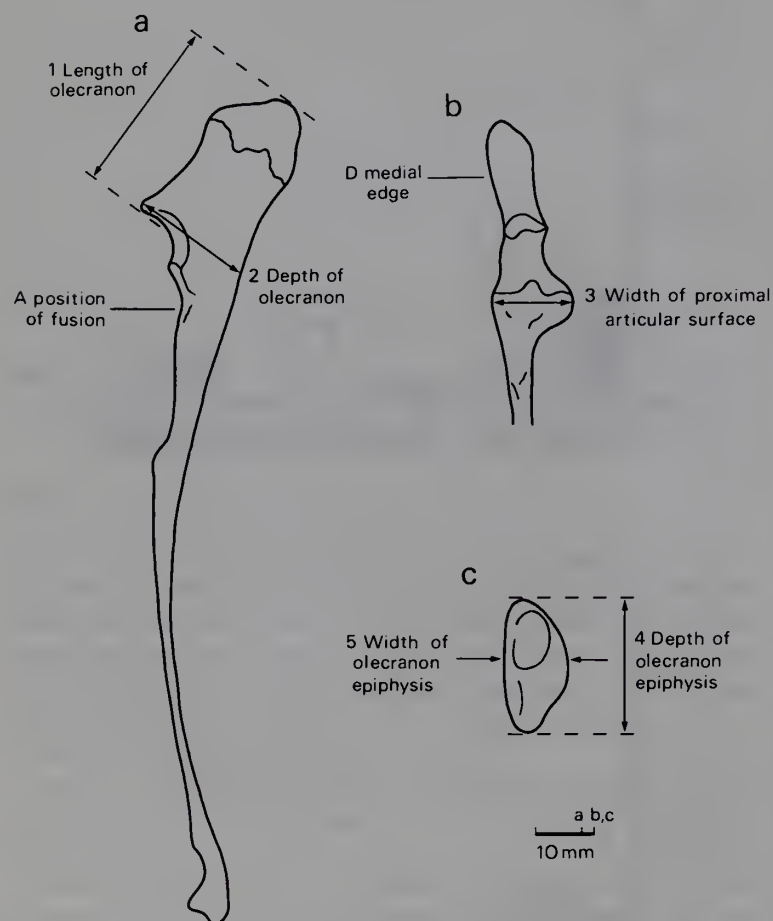


Fig. 20 Left ulna: **a** lateral view. **b** anterior view. **c** dorsal view on olecranon process. 1–5 measurements (see Appendix). A, D characters analysed in Figure 21.

which is not present in the patella of the goat (Figs 28a A, 29 A).

Talus and calcaneum

Five bones make up the tarsus in the sheep, as in all Bovidae. These are the talus (often called the astragalus), the cal-

caneum, the scapho-cuboid, the large cuneiform, and the small cuneiform. Only the talus and calcaneum have been included in this study. The talus acts as a pulley and articulates with the distal end of the tibia and the scapho-cuboid as part of the hock joint.

The talus has no epiphysis but is nearly ossified before birth although there is some growth in the bone during the first year of life. The calcaneum has an epiphysis at the end of the tuber calcanei which according to Silver (1969) fuses in the sheep between 2½–3 years. It is fused in 3 out of the 6 three-year old male Soay calcanei (Fig. 2).

The mean length of the combined male and female tali is 25.21, that of the castrates is 26.63, and for the goats it is 32.66 (Fig. 28c; Appendix).

The best character for distinguishing the talus of sheep from goat is the distal end of the medial articular ridge which is weakly developed without a sharp angle in the sheep (Fig. 28d A). In the goat this ridge, in medial view, looks like a sharp point. One female and four castrate Soay tali are intermediate for this character (Fig. 29 A).

The calcaneum articulates with the posterior side of the talus and completes the pulley action of the hock joint, the whole being bound together with ligaments.

The mean length of the combined male and female calcanei is 50.62, for the castrates it is 54.57, and for the goats it is 66.27.

According to Boessneck (1969) the calcaneum of the sheep should be relatively easy to distinguish from that of goat. There are three characters that can be used. In the sheep the anterior border of the tuber calcanei is straight while it is slightly convex in the goat (Fig. 28g A) and the articular facets, which attach to the posterior side of the talus, are separate in the sheep and joined into one surface in the goat (Fig. 28f B). Both these characters are fairly consistent for the Soay calcanei but there are some intermediate bones (Fig. 29 A & B).

The third method of distinction lies in the proportion of the length of the lateral process of the calcaneum to the length of the condyle which articulates with the anterior lateral side of the talus (Fig. 28e 3:4). According to Boessneck (1969) this index should be more than 100% for the sheep and less than 100% for the goat, that is the lateral condyle is as long or longer than the lateral process in the sheep and in the goat it should be shorter than the lateral process. However it was not so for the Soay calcanei or for the small sample of goat bones from Holy Island. In these samples this proportion was found to be too variable to be distinctive. (See Appendix for summaries of measurements).

Metapodial bones

In the sheep and goat, as in all two-toed ruminants, the third and fourth metacarpal and metatarsal (metapodial) bones are extended in length and fused to form a single shaft with two distal condyles. These articulate with the phalanges which carry the two hooves on each foot. In the foetus, however, the two shafts of the metapodial bones are unfused and can be seen to be separate elements.

The proximal end of the metacarpal bone articulates with the distal ends of the carpal bones, forming the knee joint in the forelimb. The proximal end of the metatarsal bone articulates with the distal ends of the tarsal bones in the hock joint of the hindlimb.

In the wild sheep (*Ovis orientalis*) the metapodial bones are

Radius and Ulna

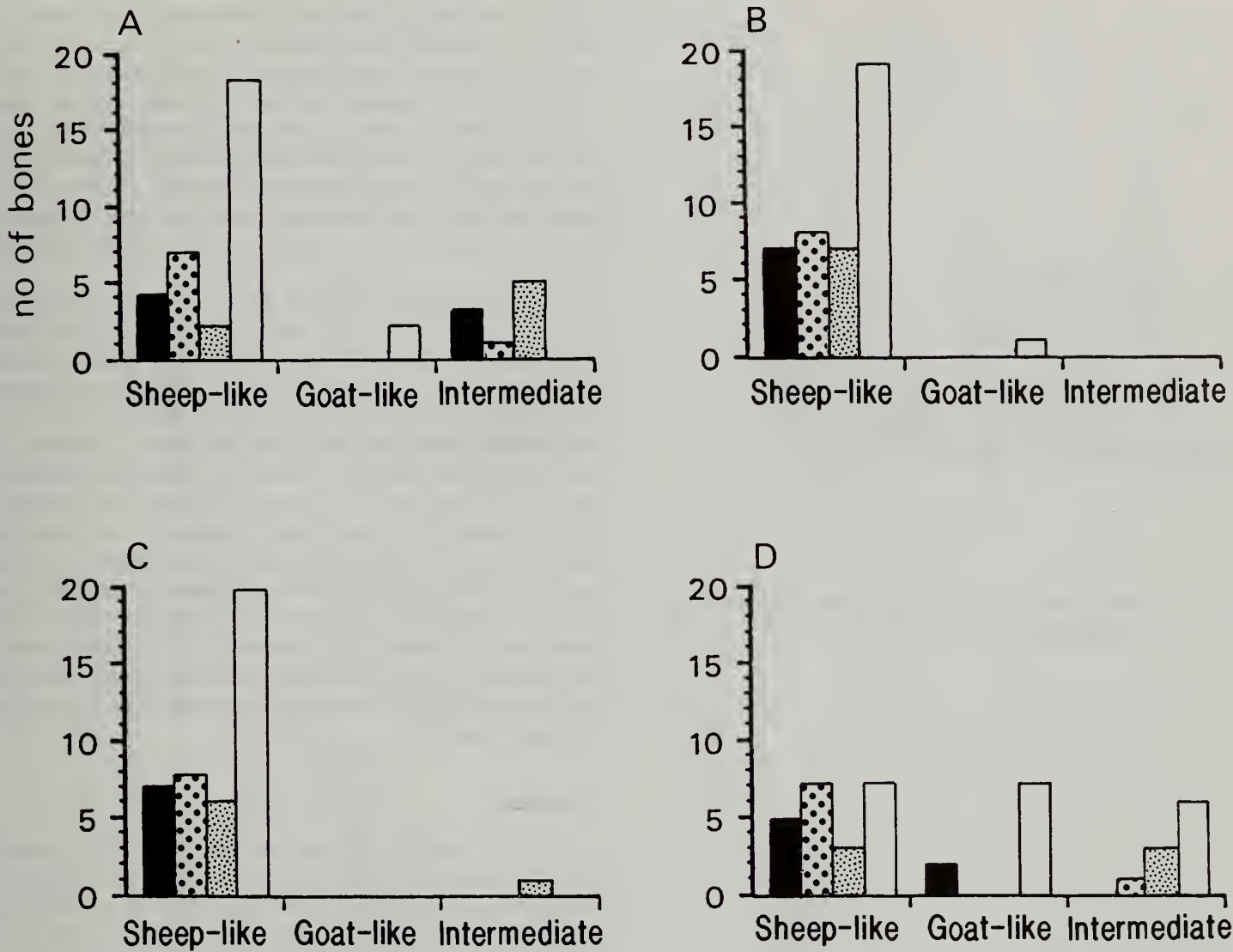


Fig. 21 Radius and ulna: analysis of sheep-like & goat-like characters. A fusion of shafts of radius and ulna: sheep—unfused; goat—fused proximally. B shape of lateral edge of proximal articular surface of radius: sheep—forms a ledge; goat—ledge absent. C shape of distal facet in radius for articulation with the scaphoid: sheep—long and narrow; goat—broad and more angular. D shape of medial edge of olecranon process of ulna: sheep—slightly convex; goat—almost straight.

long and rather like those of deer in their proportions, while in the goat the metapodial bones are shorter and more robust, especially in the metacarpal of the wild male goat (*Capra aegagrus*). These proportional differences make the wild sheep a longer-limbed, more deer-like animal than the wild goat. In the domestic caprines, however, the proportional differences have been reversed by artificial selection for short-legged sheep in north western Europe, so that in Britain goats are generally taller animals than sheep. On the other hand the bones of a castrated ram grow longer than those of the entire male so wethers will be taller than ewes or rams.

As the Soay sheep has not been subjected to artificial selection for perhaps thousands of years the body and limbs, particularly the metapodials, are relatively longer than they are in domestic breeds but they closely resemble those of early domestic sheep whose remains are found on prehistoric sites, and they are considerably longer for their width than the metapodial bones of the goat.

The mean lengths of the combined samples of male and female metapodial bones are 116.75 (metacarpals) and 126.57 (metatarsals); for the castrates the mean lengths are 127.54 (metacarpals) and 140.58 (metatarsals); and for the goats

the mean lengths are 121.32 (metacarpals) and 133.05 (metatarsals).

The proximal epiphyses of the metapodial bones fuse before birth as do the two shafts of each bone. The distal epiphyses, which at first are two separate condyles, fuse between 18–24 months, according to Silver (1969). However in the sample of Soays the one castrate of 2 years 1 month has unfused metapodial condyles and amongst the three year old males and females only four are fused (Fig. 2).

It is rather easy to distinguish the complete metapodial bones of the Soay from those of the goat by their long slender proportions although, as already stated, this does not hold good for improved breeds of sheep. If the width of the shaft is expressed as a percentage of the length of the bone then this index was never more than 13% for the Soay metacarpal and 11% for the metatarsal, while for the goat the indices were always more than 17% for the metacarpal and 12% for the metatarsal (see Appendix for summaries of the measurements).

The proximal ends of the metapodial bones are difficult to distinguish between sheep and goat, but this can sometimes be done by the presence or absence of synovial pits in the

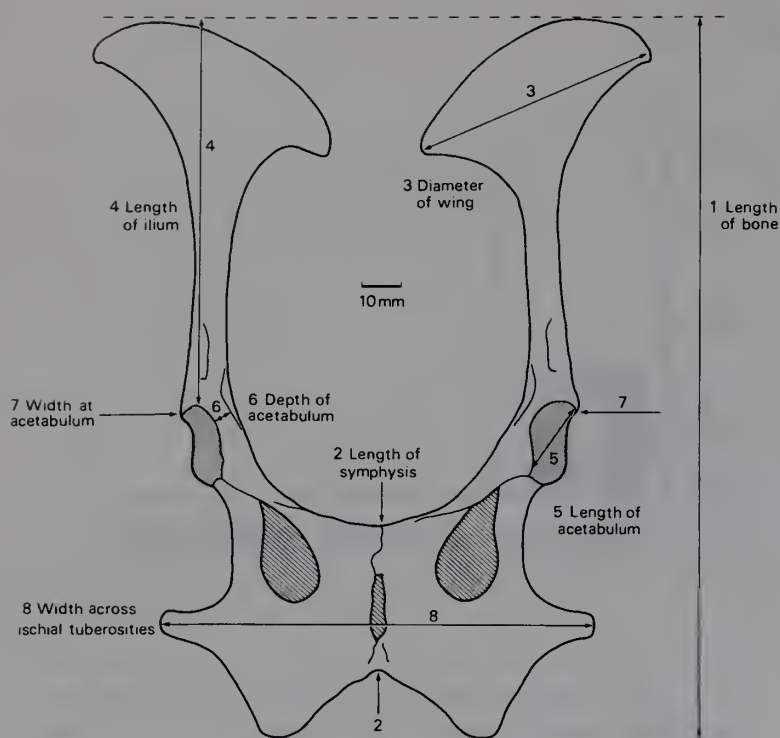


Fig. 22 Pelvis: ventral view of left and right innominate bones. 1–8 measurements (see Appendix).

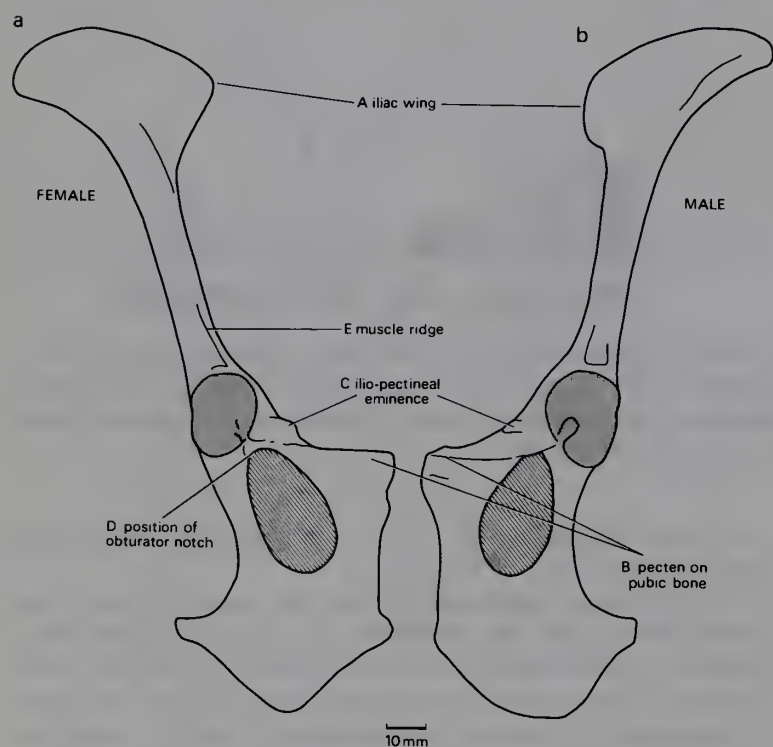


Fig. 23 Pelvis: a female—ventral view of right innominate bone. b male—ventral view of left innominate bone. A–E characters analysed in Figure 24.

articular surface (Fig. 30c A, d A). (Synovial pits or fossae are non-articular cavities in the surface of a bone which forms part of a synovial joint). Boessneck (1969) claimed that pits are rare in metacarpal bones but that they are sometimes found in goats. However, amongst the metacarpals of the Soays a high proportion have synovial pits (Fig. 31 A). In the metatarsal the situation is more complicated: in the sheep, according to Boessneck (1969) there should be no synovial pits but if present there should be only one circular hole. In the goat on the other hand there are often from one to three

strikingly large holes. Figure 31 A shows that this character is consistent for the proximal ends of the Soay metatarsal bones and there are no intermediate cases.

The distal ends of the metapodial bones are rather easier than the proximal ends to distinguish between sheep and goat. As described by Boessneck (1969) the two verticilli (whorls) of the trochlear condyles lie parallel to each other in the sheep while in the goat the medial verticillus diverges at an acute angle from the lateral verticillus (Fig. 30a B, b B). In the Soay metacarpals and metatarsals this character is fairly consistent but in both elements there are some intermediate conditions where the verticillus was at a slight angle (Fig. 31 B, B).

A second distinction in the distal condyles is determined by measurement. In the sheep the parts of the condyle peripheral to the verticilli are larger and less deeply notched than in the goat (Fig. 30e), although this is more marked in the metacarpal than in the metatarsal, and the medial trochlear condyle is larger than the lateral. If the diameter of the medial trochlear condyle is measured against the diameter of the medial verticillus (the distal depth of the condyle) the index is found to be significantly higher in the sheep metacarpal than in the goat and marginally higher in the sheep metatarsal. The index for the metacarpals of the Soay sample is never below 62% and never above 62% for the goat which agrees with the results of Boessneck (1969). The indices for the metatarsal are a minimum of 60.6% for the Soays and a maximum of 60.7% for the goat (see Appendix for summaries of measurements).

Phalanges

The sheep conforms to the normal mammalian pattern of three phalanges in each functional digit in the fore and hind limbs. The proximal end of the first phalanx articulates with the distal end of the metapodial bone and is commonly known as the fetlock, while the joint between the first and second phalanges is known as the pastern. (The third joint between the second phalanx and the hoof used to be called, in the horse, the coffin joint). There are sesamoid bones on the posterior sides at the distal ends of the metapodial bones, phalanx 1, and phalanx 2.

It is not easy in the sheep to distinguish the phalanges of the fore and hindlimb although phalanx 1 is often longer and more robust in the forelimb than it is in the hind, especially in male animals carrying heavy horns. It is relatively easy to distinguish the phalanges of sheep from those of goat on the characters described by Boessneck (1969).

PHALANX 1. The mean length of the combined male and female, fore and hind limb first phalanges of the Soays is 32.94, for the castrates it is 34.80 and for the goat it is 43.91.

In Silver (1969) there is a misprint in the table giving the fusion times of the ox and sheep first phalanges. The ages are transposed so that the proximal epiphyses should read 13–16 months (1½ years in the ox) and the distal epiphyses should read before birth for both sheep and ox instead of vice versa. In the sample of Soays the proximal epiphysis is beginning to fuse in some of the one year olds and is fully fused in all the older specimens (Fig. 2).

There are four characters that distinguish the first phalanges of sheep from those of goat. At the proximal end of the bone, in the sheep, the lateral edge of the posterior side of the bone below the proximal articular surface does not form a

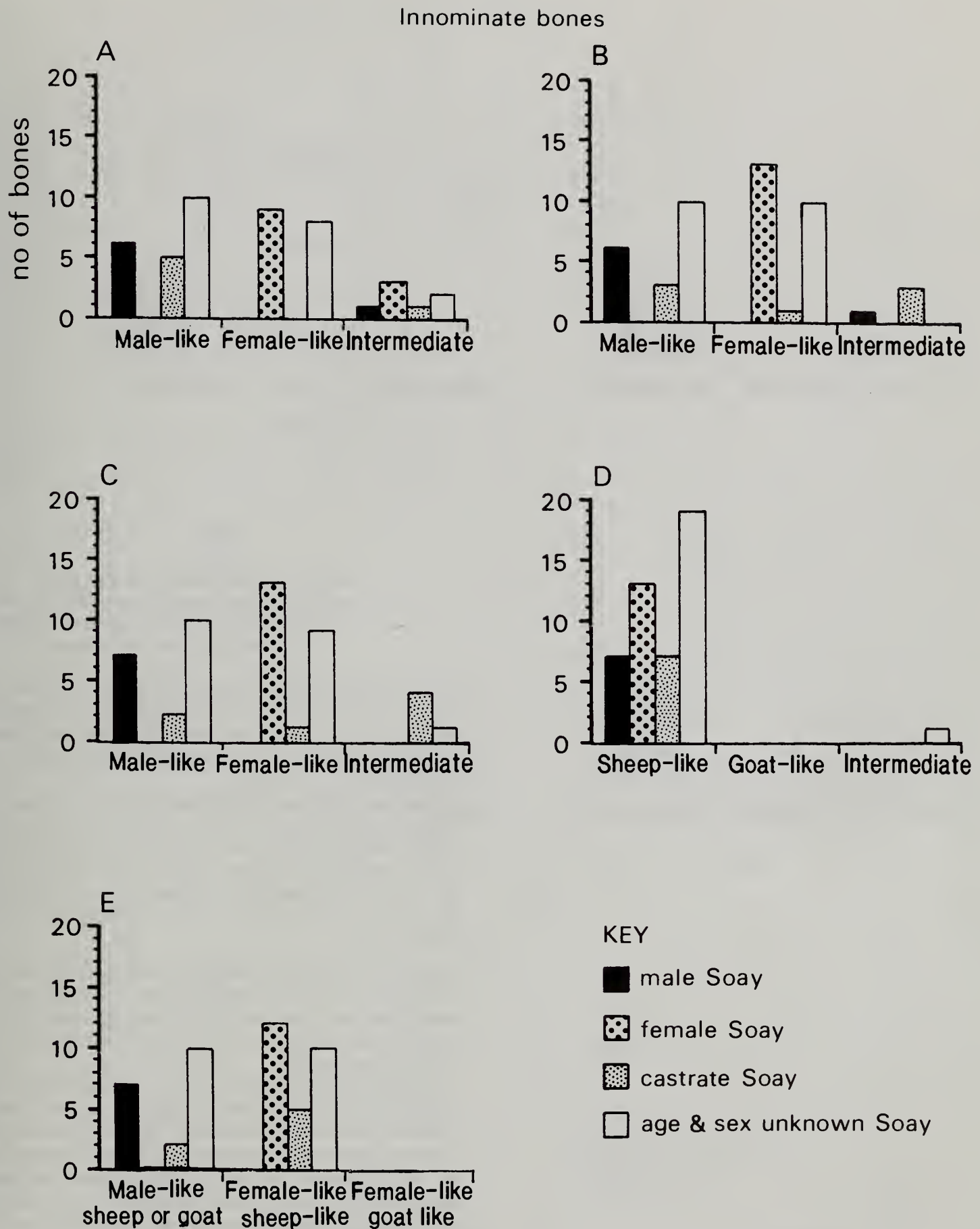


Fig. 24 Pelvis: analysis of male-like & female-like and sheep-like & goat-like characters. A shape of iliac wing: male sheep and goat—blunt and rounded; female sheep and goat—pointed. B shape of pecten: male sheep and goat—rounded and indistinct on robust pubic bone; female sheep and goat—a sharp ridge on slender pubic bone. C shape of iliopectineal eminence on pubic bone: male sheep and goat—pad-shaped; female sheep and goat—sharp-edged or pointed. D notch on anterior, dorsal border of obturator foramen: sheep—absent; goat—present. E muscle ridge on ventral body of ilium: male sheep and goat—absent; female sheep—short, narrow ridge bordering and deep pit; female goat—long, more strongly-marked ridge, shallow pit.

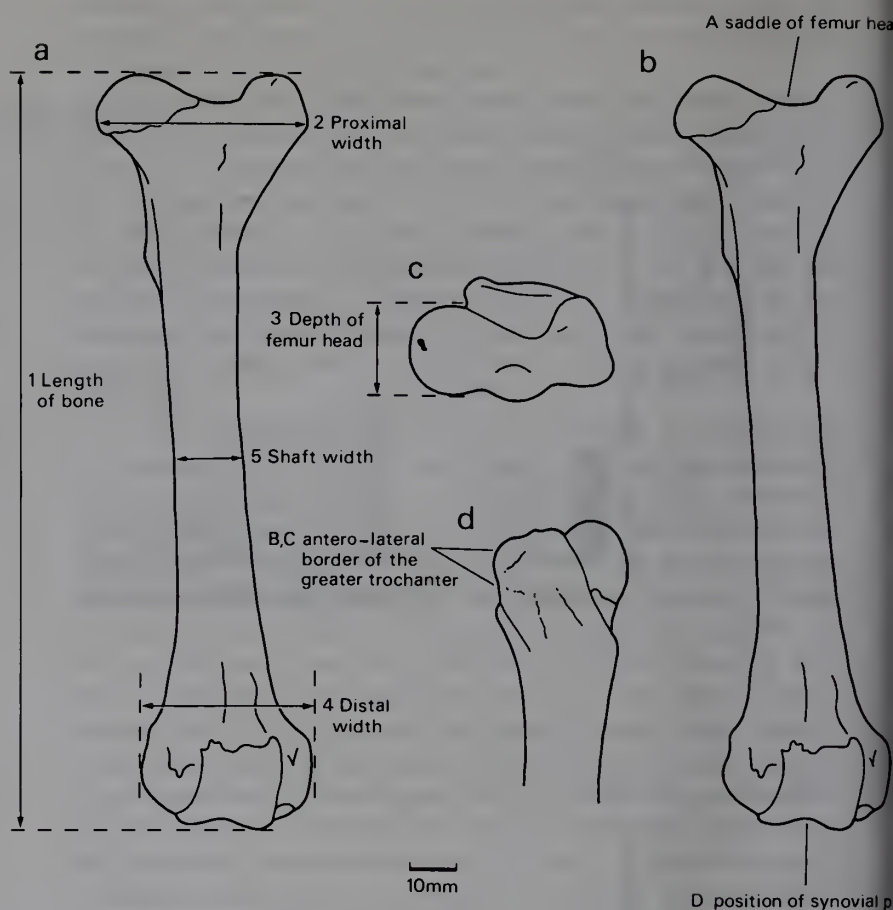


Fig 25 Left femur. **a** and **b** anterior views. **c** dorsal view of proximal articular surface. **d** lateral view of proximal end. 1-5 measurements (see Appendix).

A-D characters analysed in Figure 27.

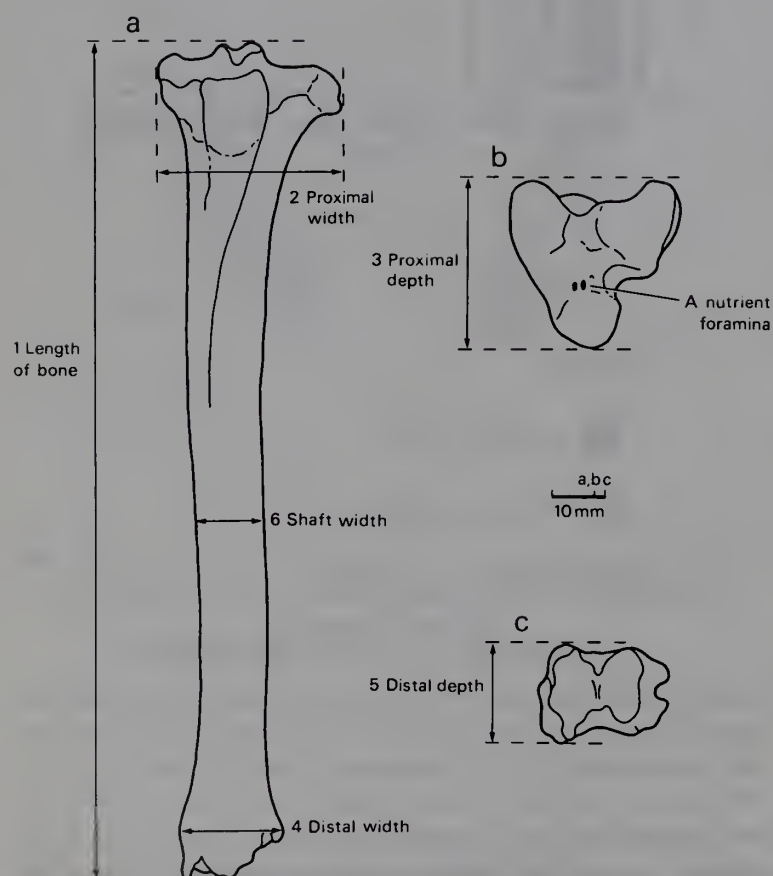


Fig 26 Left tibia: **a** anterior view. **b** dorsal view of proximal articular surface. **c** ventral view of distal articular surface. 1-6 measurements (see Appendix). A, B characters analysed in Figure 27.

ridge as it does in the goat (Fig. 32b A, d A). However this ridge was found difficult to assess and it can be seen from the results in Figure 33 A that there is a high proportion of phalanges that are either intermediate or goat-like for this character.

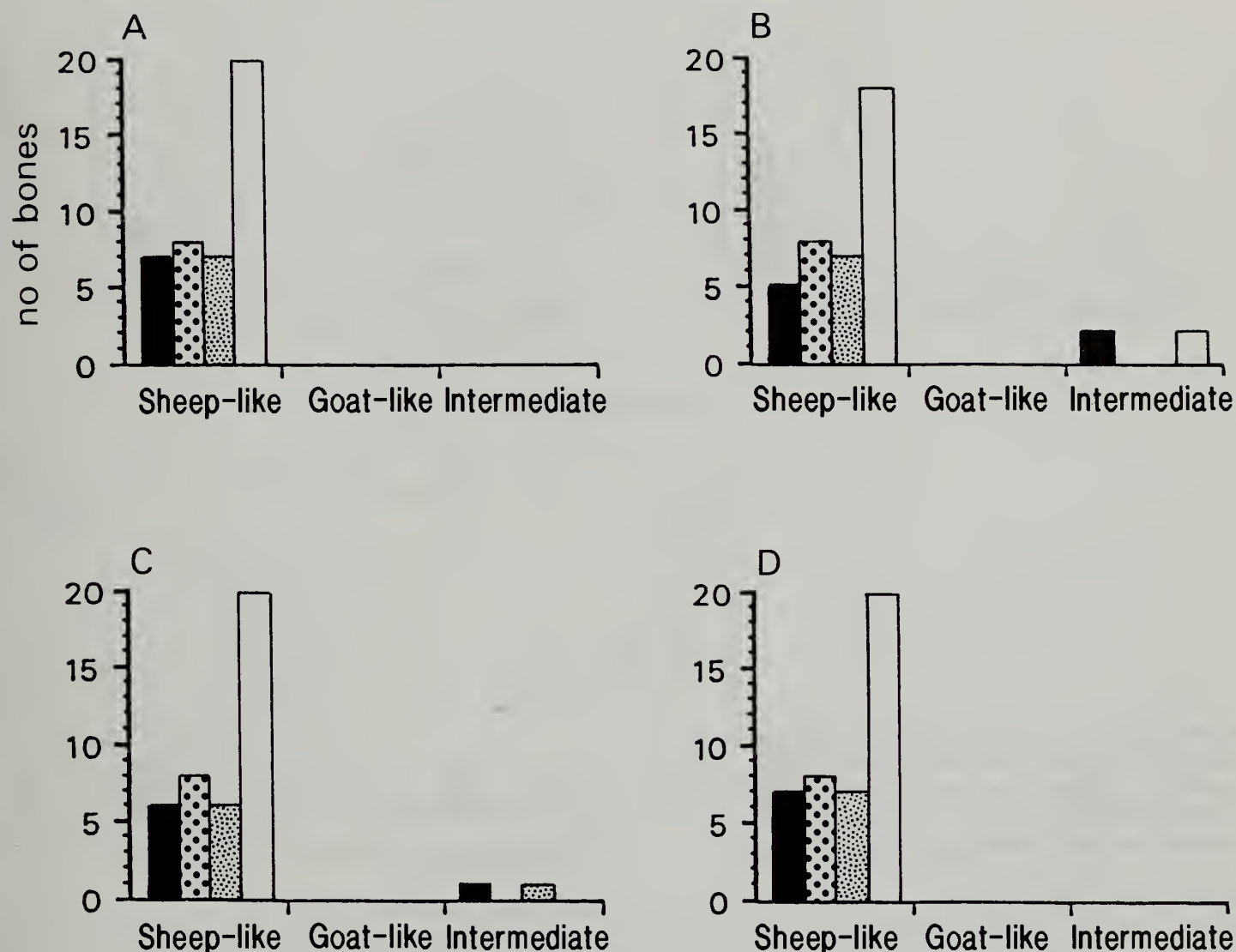
The most clear-cut differences were seen in the flat or slightly convex surface of the posterior side of the phalanx (usually concave in the goat) (Figs 32b B, 33 B), the poorly-marked muscle scars on the edges of the posterior side (Figs 32b C, d C, 33c), and most obviously the wide angle of the two halves of the posterior, distal articular surface (Figs 32b D, 33 D).

PHALANX 2. The second phalanx is about two thirds the length of the first. The mean length of the combined male and female, fore and hindlimb second phalanges of the Soays is 20.09, for the castrates it is 20.47 and for the goat it is 31.06, (Fig. 32f; Appendix).

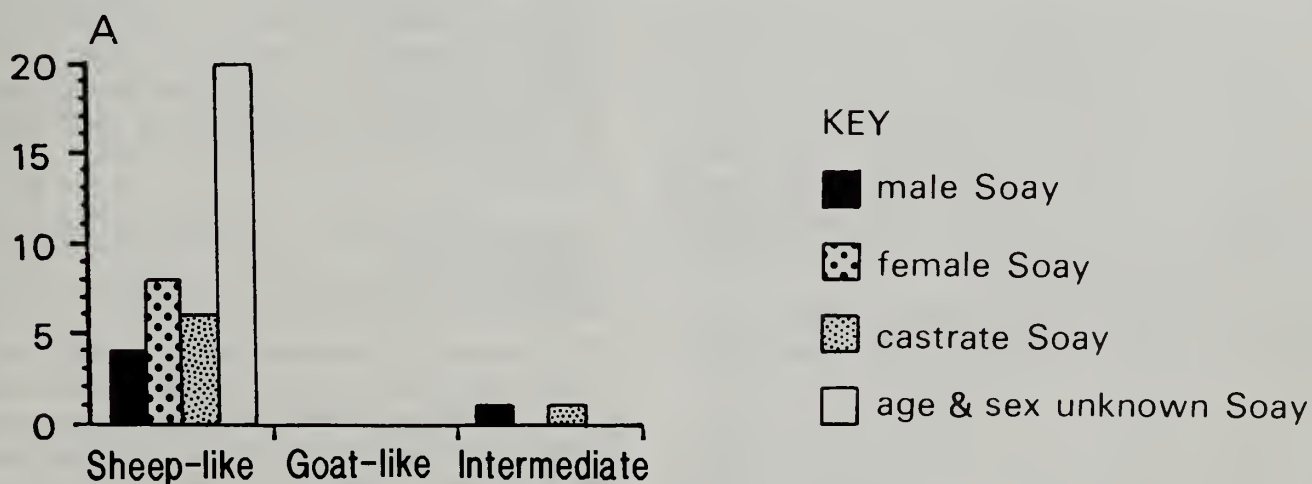
As with the first phalanx there is a transposition of the fusion ages for the proximal and distal epiphyses in the table of Silver (1969). The ages should read 13-16 months for the proximal epiphysis (1½ years for the ox) and before birth for the distal epiphysis. As with the first phalanx, the proximal epiphyses of the Soay second phalanges were beginning to fuse in the one year old elements and were fully fused in the older specimens (Fig. 2).

There is one clear distinction between the second phalanges of sheep and goat. In the sheep, including Soays, the two halves of the posterior, distal articular surface are similar in size while in the goat the medial side is drawn up into a ridge or little 'tail' (Fig. 32g A). Figure 33 A shows that only

Femur



Tibia



KEY

- male Soay
- ▤ female Soay
- ▥ castrate Soay
- age & sex unknown Soay

Fig. 27 Femur and tibia: analysis of sheep-like & goat-like characters. Femur A shape of head: sheep—extended in a medio-lateral direction across the saddle of the proximal end; goat—restricted and ball-like. B shape of antero-lateral border of greater trochanter: sheep—flat or with shallow depression; goat—slightly convex. C profile of antero-lateral border: sheep—square; goat—rounded. D synovial pit on distal trochlear: sheep—absent; goat—present. Tibia A position of nutrient foramina on proximal articular surface: sheep—one or more foramina on flat surface of epiphysis; goat—foramina are contained in a pit.

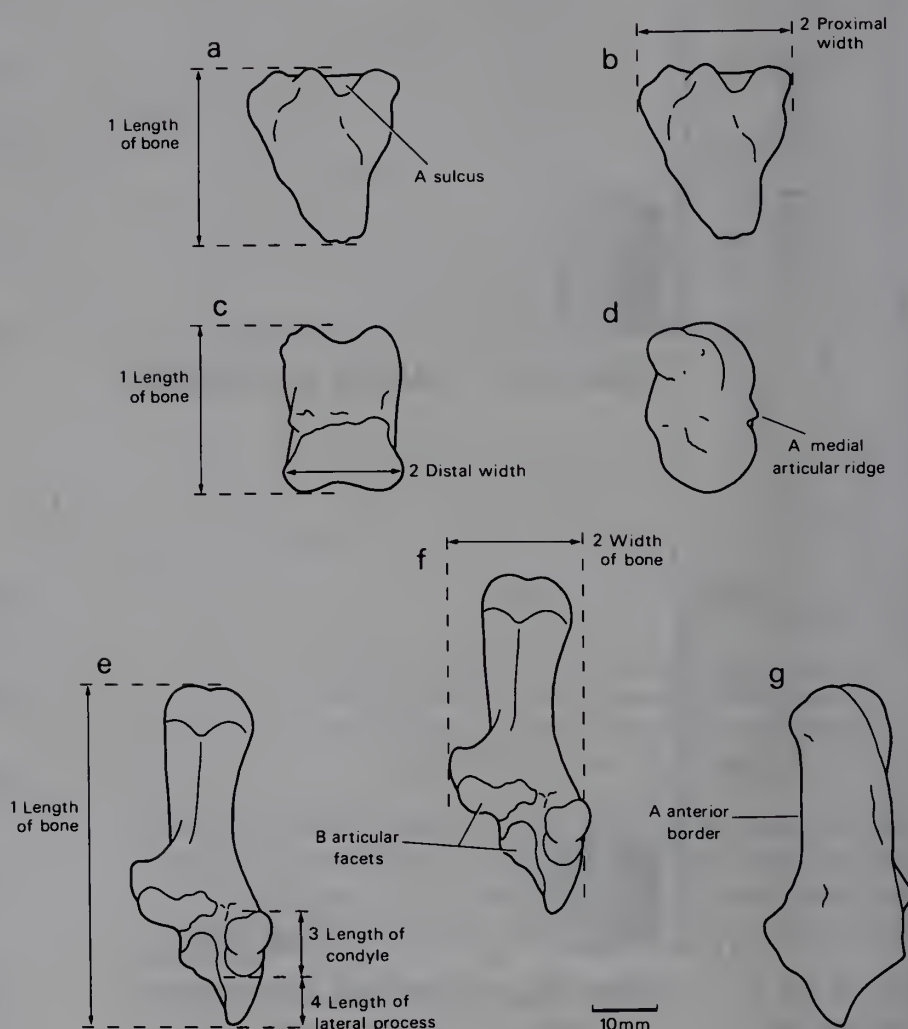


Fig. 28 Left patella, talus and calcaneum: **a** and **b** anterior view of patella. 1 and 2 measurements (see Appendix). **A** character analysed in Figure 29. **c** anterior view of talus. 1 and 2 measurements (see Appendix). **d** medial view of talus. **A** character analysed in Figure 29. **e** and **f** dorsal views of calcaneum. 1–4 measurements (see Appendix). **B** character analysed in Figure 29. **g** lateral view of calcaneum. **A** character analysed in Figure 29.

two of the Soay second phalanges are intermediate for this character.

PHALANX 3—HOOF CORE. The third phalanx is quite different in shape from the other two because it forms a core for the hoof. Its lateral side is rough, porous, and perforated by foramina while its medial side is flattened to lie as a pair against the adjacent hoof. The sole of the hoof core is slender and slightly twisted. The length of the bone is measured along the sole (Fig. 34a 1). The mean length of the combined male and female hoof cores of the Soays is 24.96, for the castrates it is 27.64, and for the goats it is 33.41.

The bone has no epiphysis and is partly ossified at birth which explains why newborn sheep and other hoofed mammals have very large feet for their overall size at birth.

The hoof core of sheep is easily distinguished from that of the goat, in which it is a narrower and sharper bone. Four characters were used in the analysis of the Soays, of which all but the first proved to be sound. The round blunt dorsal edge of the bone, as described by Boessneck for sheep is not seen clearly in the Soay hoof cores (Figs 34b A, 35 A) and it may be that these sheep have narrower hooves than the improved breeds, in adaptation to their rocky environment. A small

proportion of hoof cores is intermediate for the second character which is a larger extensor process coming down into a hollow or saddle, whereas in the goat the profile is continuous and convex (Figs 34b B, 35 B). The third and fourth characters, which are a convex lateral edge to the sole and a concave medial edge are consistent discriminants with only one element being intermediate (Figs 34a C, a D, 35 C D).

DISCUSSION

The purpose of this work is to provide a comprehensive description of the skeleton of a single breed of sheep with a set of measurements for each skeletal element and to test the criteria for distinguishing sheep bones from goat bones in material from archaeological sites. In addition the effects of castration in the male have been investigated.

The distinction between sheep and goat remains on archaeological sites is of considerable importance for the interpretation of the palaeoeconomy and palaeoecology of the site. For example from the Neolithic site of the Links of Noltland on

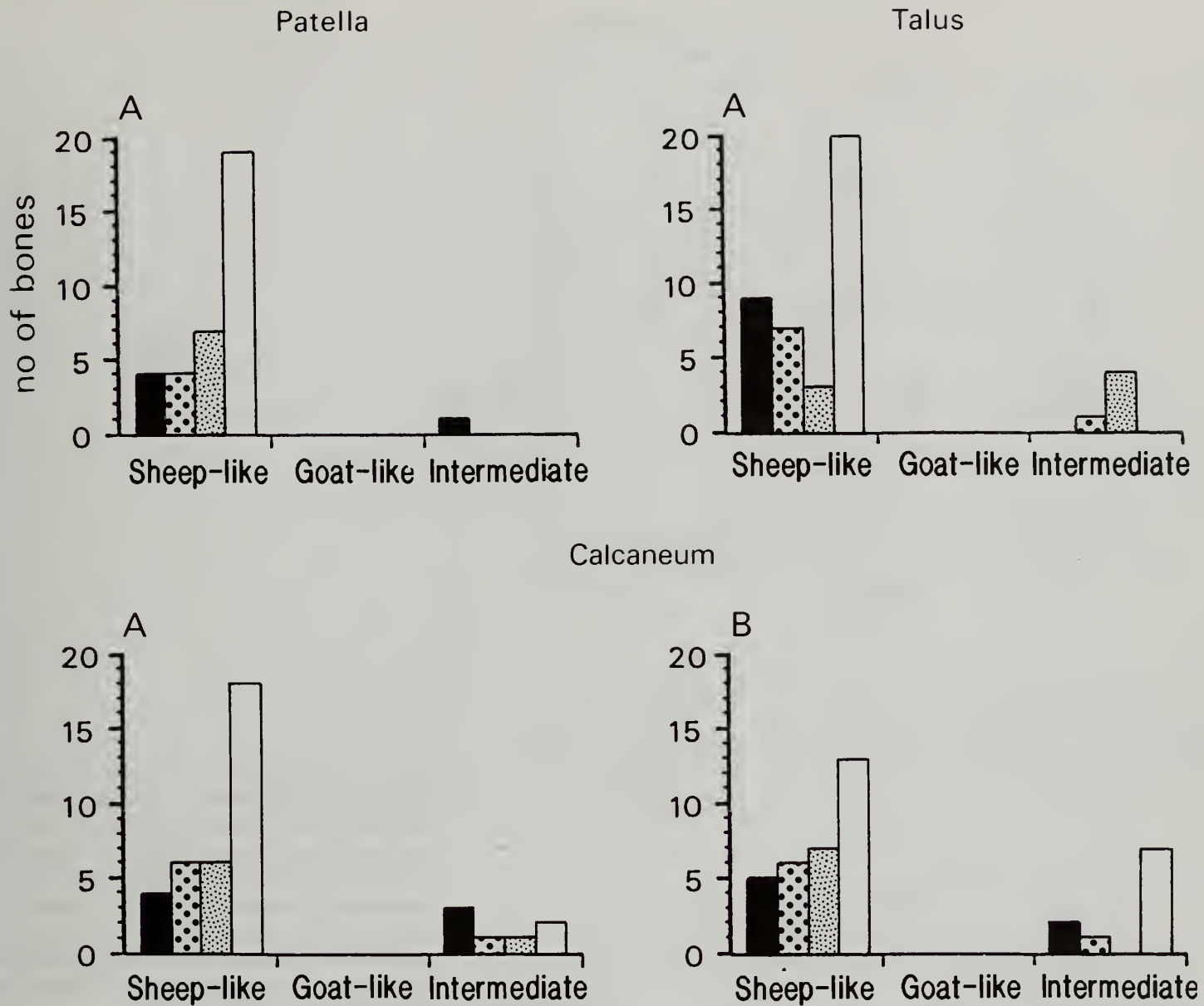


Fig. 29 Patella, talus, and calcaneum: analysis of sheep-like and goat-like characters. Patella: A sulcus on antero-proximal side: sheep—present; goat—absent or small. Talus: A shape of distal end of medial articular ridge: sheep—weakly developed and without a sharp angle; goat—drawn into a point and strongly developed. Calcaneum: A shape of anterior border: sheep—straight; goat—convex. B shape of articular facets for the posterior side of the talus: sheep—separated into two parts; goat—a single facet.

the island of Westray, Orkney, no goat remains have been identified; the economy was unusual for the Neolithic in being based mostly on sheep with a few cattle, pigs, and red deer adding to the meat-supply, which was also supplemented by fish and perhaps some whale and seal meat (Armour-Chelu, in prep.). There is no evidence (such as artefacts for spinning or weaving) for the use of wool from these Neolithic sheep but they may have been milked.

From another Neolithic site, that of Yvonand IV, a typical lake village site on the shore of Lake Neuchâtel in Switzerland, 5021 elements were identified to species. There were 66 bones of sheep (1.3% of the total number of identified elements); 35 bones of goat (0.7%); and 184 elements that were sheep or goat (3.7%). So here, it seems there were approximately twice as many sheep as goats but caprines as a whole were an insignificant part of the meat-supply which was mostly obtained from cattle and pigs, as is usual for the Neolithic in Europe (Clutton-Brock, 1990).

In contrast, Neolithic sites in western Asia usually provide a preponderance of sheep and goat remains over other livestock, and goats are usually in greater numbers than sheep.

Although the aim should be to discriminate between as many elements of sheep and goat as possible, from any site there will always be a very large number of fragments that can only be ascribed to the category 'sheep or goat' because the characters for distinction will be broken away.

Sometimes it is possible to interpret details of human social life or tradition from the proportions of the different taxa represented by the animal remains. For example in the Middle Bronze Age at the famous site of Jericho (Israel) the great majority of the bones from the Tell (the habitation site) were from goats, whereas those from the tombs were from sheep which may have been considered as higher-status animals only to be killed for sacrifices (Clutton-Brock, in prep).

The work of Boessneck *et al.* (1964) on several hundred skeletons of sheep and goats has shown that the improved breeds retain their generic characteristics, but the size and proportions of the bones have been greatly altered by selective breeding.

The wild ancestor of all domestic sheep (*Ovis orientalis*) is a long-legged, fine-limbed artiodactyl, more deer-like and with

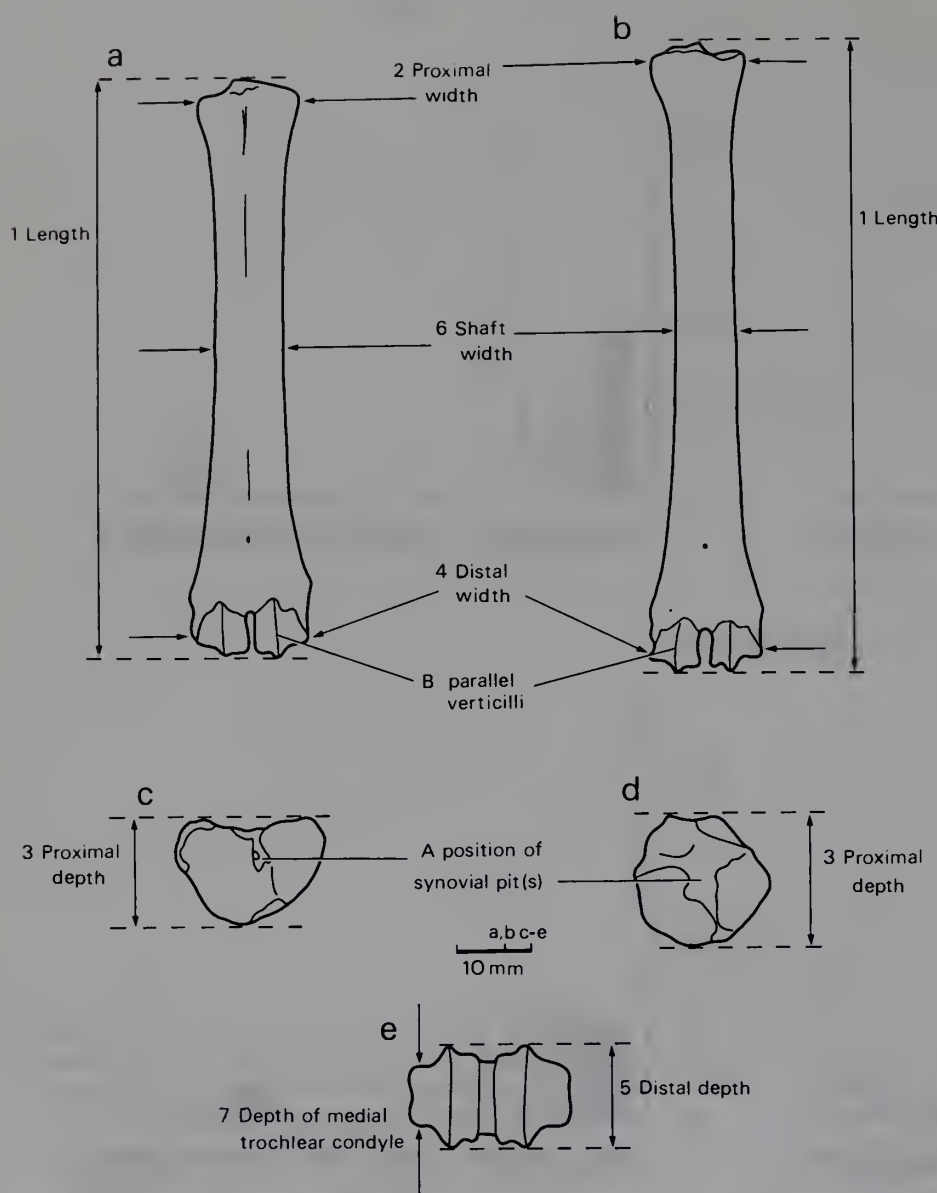


Fig. 30 Left metapodial bones: **a** and **b** anterior views of metacarpal and metatarsal. 1, 2, 4, 6 measurements (see Appendix). **B** character analysed in Figure 31 (metacarpal B and metatarsal B). **c** and **d** dorsal views of anterior articular surface of metacarpal and metatarsal. 3 measurement (see Appendix). **A** character analysed in Figure 31 (metacarpal A and metatarsal A). **e** ventral view of distal articular condyles of metacarpal/metatarsal. 5, 7 measurements (see Appendix).

longer limbs than the wild ancestor of the domestic goat (*Capra aegagrus*). Modern north European sheep have a barrel-shaped body and short thick-set limbs that are usually shorter than those of domestic goats which have been less influenced by artificial selection for meat quality. Because of these changes in the skeleton of the improved breeds of sheep it has been usual, since the time of Pitt-Rivers (1899), to use the Soay as a model of primitive domestic sheep for comparison with the remains of prehistoric sheep. Despite this use, no metrical or morphological analysis of the Soay has ever been undertaken until the present work.

We have found that although the Soay is a small fine-limbed sheep the legs are relatively and absolutely shorter than they were in the Neolithic sheep from the Links of Noltland on Westray, Orkney. This can be seen from Table 8 which gives the dimensions of the complete radii, metacarpals, and metatarsals from Noltland to compare with the dimensions of the same bones from the Soays, presented in the Appendix.

Two explanations for the shorter legs of the Soay may be suggested: either, these sheep had reached a later stage in domestication than the Noltland sheep before they were taken to the islands of St Kilda, or the shortening of the legs has occurred as a secondary adaptation to the particular selective pressures associated with survival on small islands.

In this context it is of interest to look at the work of Groves (1989) and Pees & Hemmer (1980) on the cranial capacities of living sheep. They found that the cranial capacity of the wild *Ovis orientalis* was slightly higher than that of the Corsico-Sardinian mouflon (*Ovis musimon*) which in turn was higher than the cranial capacity of domestic breeds. The Soay fell into the range of domestic sheep. This was to be expected as wild species normally have a higher cranial capacity than their domestic counterparts, and it is now generally accepted that the Corsico-Sardinian mouflon is an anciently feral sheep descended from very early domestic stock taken to the Mediterranean region from western Asia sometime around 7500 years ago (Geddes, 1984; Poplin, 1979). These sheep are closer to the wild *Ovis orientalis* than is the Soay not only in their cranial capacity but also in their longer limbs and in their wild-type pelage (see p. 3).

The conclusions that can be drawn from our very careful assessment of the characters of Boessneck *et al.* (1984) and Boessneck (1969) for the discrimination of sheep from goat bones are that there are very few characters, used on their own, on which a valid separation can be made. The following list of characters are those which, in the analysis presented here, fall only into the sheep-like category with no goat-like or intermediate specimens:

skull—presence of a lacrimal fossa; axis vertebra—presence

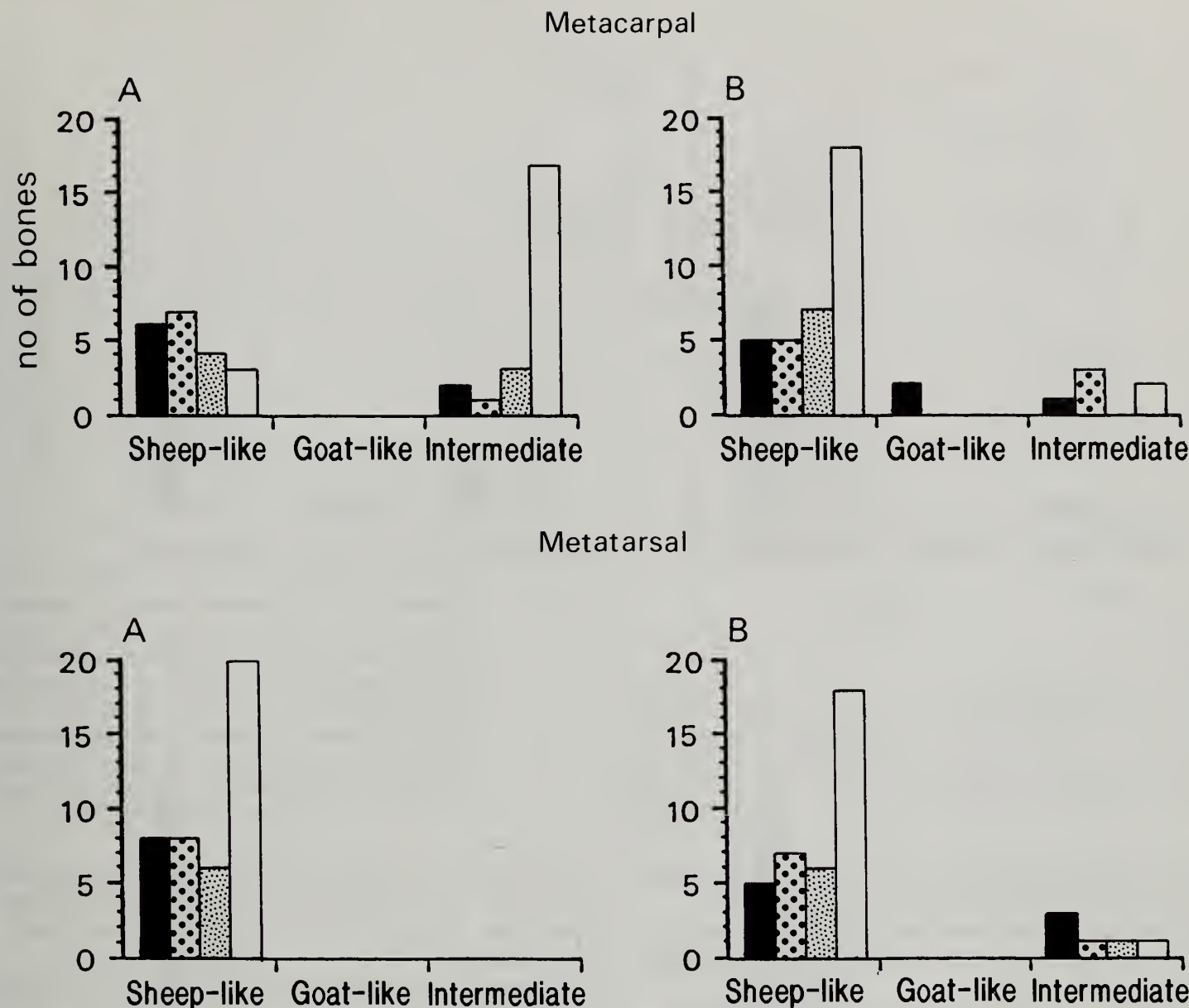


Fig. 31 Metapodial bones: analysis of sheep-like & goat-like characters. A Synovial pits on the proximal articular surface: sheep—absent in the metacarpal, rare in the metatarsal or if present there is one large circular hole; goat—sometimes present in the metacarpal, often present in the metatarsal. B angle of the verticilli of the distal condyles: sheep—lie parallel to each other in metacarpal and metatarsal; goat—the medial verticillus lies at an acute angle to the lateral verticillus in metacarpal and metatarsal.

of a transverse canal; scapula—concave anterior margin; femur—the head forms a continuum with the saddle at the proximal end and there are no synovial pits in the distal end; metatarsal—no synovial pit in the proximal end or if present only one circular hole; hoof core—concave profile to the medial edge of the sole.

It has long been held by archaeozoologists that many features of sheep bones, in addition to those mentioned above, are diagnostic. In the Soays, however, these are compromised by a few indeterminate examples. The features in question are as follows:

SKULL: the distinctive Y-shape of the frontal-parietal suture is not seen in one skull; the lambdoid suture is not straight but is intermediate in several skulls; and the temporal fossae are not convincingly wide apart in four skulls.

SCAPULA: the presence of a pecten on the posterior margin should be diagnostic of sheep; while no Soay scapulae are allocated as goat-like, four bones are intermediate.

HUMERUS: usually regarded as a particularly distinctive bone for each species; at the proximal end the lateral tuberosity

should be broad and upright but three castrates are equivocal; the nutrient foramen should be at the back of the shaft but several are in the goat-like position on the side and two are intermediate; at the distal end the rounded epicondyle is usually considered to be one of the best sheep-like characters but two bones are intermediate.

RADIUS AND ULNA: these bones are usually unfused in the sheep and fused at the proximal ends of the shafts in the goat, but this distinction does not hold for a considerable number of the Soay elements one of which is fused and several are intermediate; the little ledge on the lateral border of the proximal end of the radius should be a diagnostic feature of sheep but it is absent in one bone.

PELVIS: the obdurator foramen should have no notch at its anterior end in the sheep but there is a slight notch in one Soay specimen.

FEMUR: the greater trochanter on the proximal epiphysis usually has a flat top and a square edge in the sheep but a few Soays are intermediate between sheep and goat for this character.

TALUS: in the sheep the medial articular ridge should be only

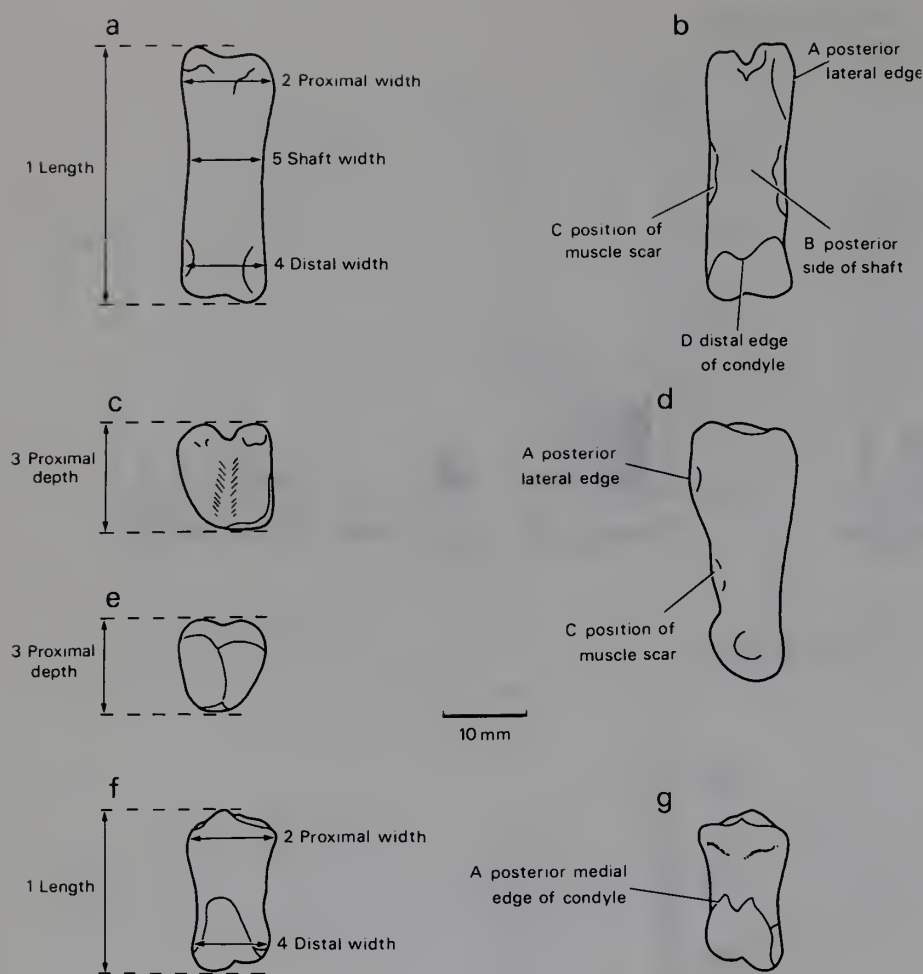


Fig. 32 Fore/hind phalanx 1 and 2: **a** anterior view of phalanx 1. 1, 2, 4, 5 measurements (see Appendix). **b** posterior view of phalanx 1; **d** lateral view of phalanx 1. A—D characters analysed in Figure 33. **c** dorsal view of proximal articular surface of phalanx 1. 3 measurement (see Appendix). **e** dorsal view of proximal articular surface of phalanx 2. 3 measurement (see Appendix). **f** anterior view of phalanx 2. 1, 2, 4 measurements (see Appendix). **g** posterior view of phalanx 2. A character analysed in Figure 33.

a weakly-developed bump but in five bones it is pointed enough for them to be classed as intermediate.

CALCANEUM: the articular facets are said to be separate in the sheep but a number of the Soay elements exhibit some degree of fusion.

METAPODIAL BONES: the verticilli on the distal condyles are expected to be parallel to each other in the sheep while in the goat the medial verticillus diverges, but in one Soay this character is goat-like and in a number it is intermediate.

PHALANX 1: the shape of this element is usually quite distinctive in the sheep and goat but in the Soays the discrimination is not clear-cut for several of the characters, which may be due to the particularly active life of these sheep.

PHALANX 2: the best character for discrimination is the symmetry of the posterior side of the distal condyle and this does apply well in the Soays except for two intermediates.

PHALANX 3 (HOOF CORE): the distinctive features noted by Boessneck, the rounded dorsal edge and the development of the extensor process are not found in the Soays while the convex lateral edge is compromised by one intermediate hoof core.

Most of the measurement ratios quoted by Boessneck were tried out on the Soay bones but they were not all found to be good discriminants; those that are useful are discussed in the text.

Each character in the analysis was tested on the male, female, and castrate samples as well as on the elements of unknown sex. However, the sex of the elements does not appear to affect the discriminant features except that some are poorly defined in the castrates. To take one example, the shape of the lateral tuberosity at the proximal end of the

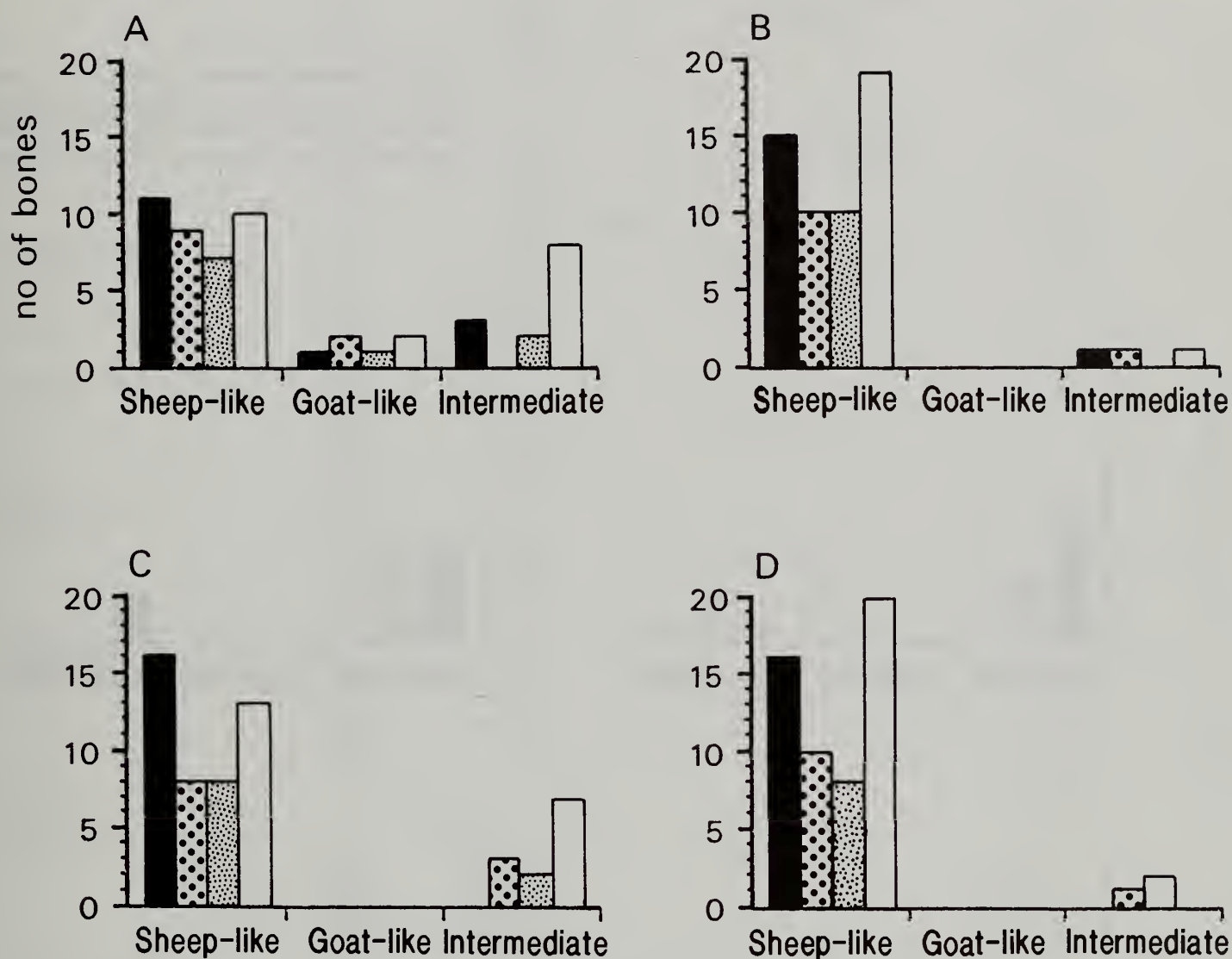
humerus is generally considered to be a sound character for distinction and in the analysis all the bones fall into the sheep-like category except for three castrates which are intermediate.

Sex-related characters were examined in the atlas, axis, and pelvis. The atlas is less reliable as an indicator of sex or genus than expected and these vertebrae in the Soays exhibit all possible interpretations. On the other hand in the axis the development of the ventral crest is a good discriminant for male sheep but is not very useful because female sheep cannot be separated from female goats on this character. In the pelvis the shape of the iliac wing is a reliable determinant for the male Soays but is less so for the females. The sex difference in the shape of the pecten that develops on the pubic bone permits clear allocation to male or female but in the castrates the pecten is indeterminate. The ilio-pectineal eminence gives a reliable and absolute distinction between male and female but again it is intermediate in the castrates.

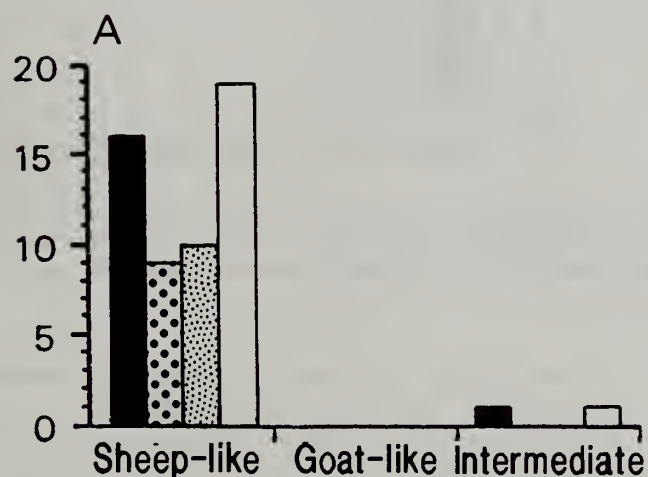
This analysis of the characters that are used to divide sheep bones from those of goats, and males from females, appears to show that many of the discriminants are unreliable but it should not be assumed that the task of separating the elements retrieved from archaeological excavation is too difficult to be attempted. When used in conjunction, and together with the proportional differences ascertained by measurement, it is possible to make specific identifications with a high degree of confidence.

A significant conclusion to be drawn from this osteological study concerns the age of skeletal maturity characterized by the complete fusion of the epiphyses in the limb bones (Fig. 2). Contrary to the widely-held theory that primitive breeds like the Soay are retarded in the times of epiphysial fusion

Phalanx 1



Phalanx 2



KEY

- male Soay
- ▤ female Soay
- ▨ castrate Soay
- age & sex unknown Soay

Fig. 33 Fore/hind phalanx 1 and 2: analysis of sheep-like & goat-like characters. Phalanx 1: A shape of lateral edge below proximal articular surface: sheep—rounded without a ridge; goat—forms a ridge. B shape of posterior side of shaft: sheep—flat or convex; goat—concave. C development of muscle scars on posterior mid-shaft: sheep—weak; goat—more strongly developed. D shape of posterior edge of distal articular condyle: sheep—has a wide open or obtuse angle; goat—has an acute or right angle. Phalanx 2: A shape of posterior medial edge of distal articular condyle: sheep—equal in height to the posterior lateral edge; goat—drawn up into a little tail.

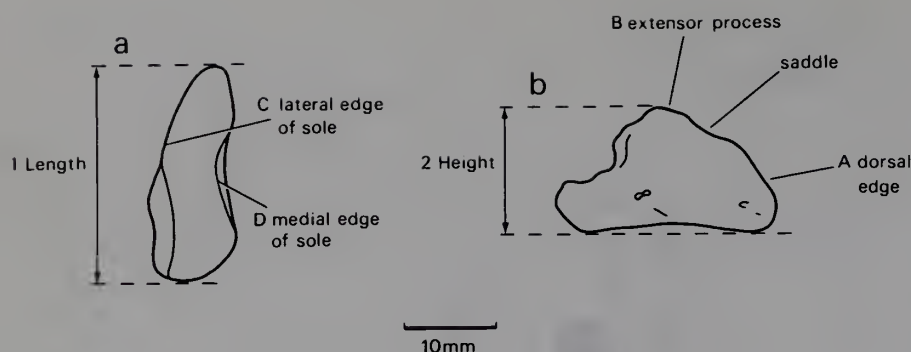


Fig. 34 Fore/hind phalanx 3 or hoof core: **a** ventral view. 1 measurement (see Appendix). C, D characters analysed in Figure 35. **b** lateral view. 2 measurement (see Appendix). A, B characters analysed in Figure 35.

Hoof core

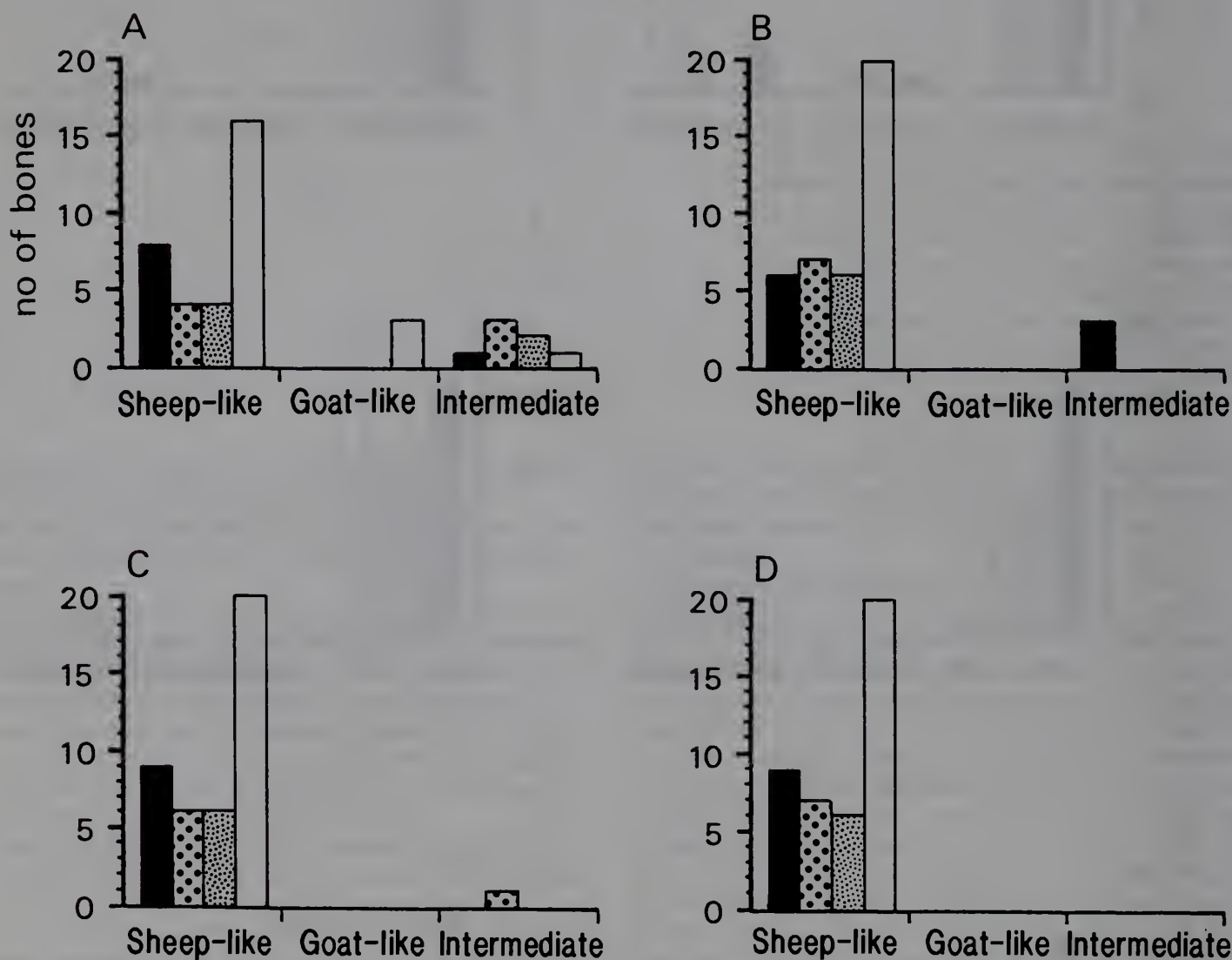


Fig. 35 Fore/hind phalanx 3 or hoof core: analysis of sheep-like & goat-like characters. A shape of dorsal edge: sheep—rounded and blunt; goat—medio-laterally flattened, sharp and pointed. B shape of extensor process: sheep—large and with a saddle or hollow in front of it; goat—small and with no saddle. C shape of lateral edge of sole: sheep—convex; goat—straight. D shape of medial edge of sole: sheep—concave; goat—straight.

compared with improved sheep, it has been found that the time of complete fusion (between three and three and a half years, see Fig. 2) is comparable to the time taken in breeds such as the Southdown that have been developed specially for early fattening.

It is interesting that another primitive breed, the Gotlandic sheep studied by Hatting (1983), also exhibited skeletal maturity at the unexpectedly early age of two and a half years.

From the work of Hammond (1940) and other researchers it is evident that the early livestock improvers and their successors, while shortening the limbs and altering the normal sequence in the development of fat and muscle, in no way affected the rate of skeletal development; so that in both improved and unimproved (including primitive) breeds of sheep epiphyseal fusion takes place at the same ages. Viewed in this light, the findings of the present study, as well as those of Hatting, do not seem so anomalous. This has important

Table 8 Dimensions (in mm) of radii, metacarpals and metatarsals of sheep from the Neolithic site of the Links of Noltland, Westray, Orkney.

RADIUS			METATARSAL		
1 Length of bone	No	16	1 Length of bone	No	12
	max	174.1		max	145.02
	min	131.38		min	125.68
	mean	149.73		mean	135.00
	st.dev	10.98		st.dev	6.26
2 Proximal width	No	16	2 Proximal width	No	12
	max	32.37		max	21.75
	min	26.82		min	16.86
	mean	30.03		mean	18.88
	st.dev	1.51		st.dev	1.5
3 Proximal depth	No	16	3 Proximal depth	No	11
	max	16.82		max	21.2
	min	14.12		min	17.54
	mean	15.58		mean	19.23
	st.dev	0.78		st.dev	1.02
4 Distal width	No	16	4 Distal width	No	12
	max	29.75		max	24.28
	min	24.66		min	20.72
	mean	27.41		mean	22.58
	st. dev	1.51		st.dev	0.96
5 Distal depth	No	16	5 Distal depth	No	12
	max	20.98		max	16.91
	min	16.57		min	14.48
	mean	18.41		mean	15.55
	st.dev	1.22		st.dev	0.77
6 Shaft width	No	16	6 Shaft width	No	12
	max	18.24		max	11.67
	min	13.24		min	10.08
	mean	16.1		mean	10.49
	st.dev	1.29		st.dev	0.55
METACARPAL					
1 Length of bone	No	13	7 Depth of medial trochlear condyle	No	13
	max	134.5		max	12.12
	min	112.62		min	10.22
	mean	125.57		mean	11.50
	st. dev	6.29		st.dev	0.54
2 Proximal width	No	12			
	max	23.94			
	min	19.96			
	mean	21.56			
	st.dev	0.95			
3 Proximal depth	No	12			
	max	16.92			
	min	15.04			
	mean	16.19			
	st.dev	0.51			
4 Distal width	No	12			
	max	26.57			
	min	22.06			
	mean	25.02			
	st.dev	1.22			
5 Distal depth	No	13			
	max	16.56			
	min	13.3			
	mean	15.45			
	st.dev	0.86			
6 Shaft width	No	12			
	max	14.1			
	min	11.28			
	mean	12.7			
	st.dev	0.82			

implications for research into ancient practices of livestock husbandry, for it has been held that modern fusion data from improved breeds cannot be directly applied to the interpretation of sheep bones recovered from archaeological contexts earlier than the late 18th century. This view is contradicted by this study.

The collections of skeletal material from the carcasses of Soay sheep that had lived wild on the island of Hirta, St Kilda, provided the impetus for this study. Perhaps a main result has been to reveal how very many questions about the morphology and development of the skeletons of mammals still remain to be answered. Very little is known about the effects of castration on the skeleton and only very preliminary studies have been carried out on the side-effects of selection for meat-quality in sheep. For example the short report of Purser (1980) on the correlation between the shortening of the cannon bone (metacarpal) of the leg and reduction of prolificacy in ewes and fatness in wethers clearly requires further investigation. The skeletons of Soay sheep combined with data on their meat-quality and breeding success could provide a 'control' for such investigations.

It is intended that the summaries of measurements of the Soay bones and the analysis of the characters that distinguish sheep from goats, which are presented here, should be used as a data-base by archaeozoologists. The complete set of measurements are held as an archive in the British Museum (Natural History) and are available to research workers, on request, as are the collections of skeletal material for further direct study.

ACKNOWLEDGEMENTS. We are indebted to members of the Mammal Section at the British Museum (Natural History) and the Department of Veterinary Anatomy of Cambridge University who prepared and curated the skeletons of the Soay sheep for this project. The material was collected from Hirta, St. Kilda by Peter Jewell in the course of his field work which was assisted in part by grants from the Leverhulme Trust, the National Geographic Society and St. John's College, Cambridge, and by Philip Armitage in 1979 with the generous assistance of a grant from the Godman Exploration Fund through the British Museum (Natural History).

We should like to thank Sheila Cameron for collecting, preparing, and presenting to the BM(NH) the skeletal material of feral goats from Holy Island, Arran, and our thanks are also due to Valerie Hardman and Derek Harvey for help with collection of the data while they were employed at the museum on vacation studentships. We thank Miranda Armour-Chelu for help with measurements and for allowing us to publish her measurements of sheep limb bones from the site of the Links of Noltland, Westray, Orkney. We thank Sebastian Payne for his measurements of male Soays from Babraham, Cambridge.

Alan Patterson and Kay Shaw, Biometrics Section, BM(NH) assisted with the computer analysis of the measurements and Harry Taylor, photographic unit BM(NH), took the photographs. The manuscript was typed by Margaret Twinn in the Physiological Laboratory, University of Cambridge, and Mrs Dee Hughes helped with the lettering of the Figures.

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Manuscript accepted for publication 18 November, 1988

APPENDIX

Summaries of the measurements of skeletal elements of Soay sheep (*Ovis aries*) from Hirta, St. Kilda, Soay castrates from Cambridge, and feral goats (*Capra hircus*) from Holy Island, Arran, Scotland. The numbers that precede the description of each measurement refer to the dimension between the points depicted on each element in the Figures. All measurements are in mm.

HORNCORES

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male not aged	Soay Female not aged	Goat Male not aged	Goat Female not aged
No in sample		11	8	5	10	8	1	1
1 Length of	max	282.00	88.00	131.00	263.00	98.00	283.00	170.00
outer curve	min	164.00	65.00	5.10	162.00	12.00		
of horn core								
2 Basal	max	166.00	82.00	106.00	143.00	82.00		
circumference	min	102.00	68.00	60.10	127.80	34.00		

SKULL

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male not aged	Soay Female not aged	Goat Male not aged	Goat Female not aged
No in sample		12 ¹	12 ²	6 ³	10 ⁴	13 ⁵	1	1
1 Condyle—	max	206.40	203.60	225.60	209.90	216.00	—	216.90
basal length	min	189.50	187.30	215.90	190.30	186.90		
	mean	197.99	195.07	220.42	198.14	195.91		
	st.dev	5.20	4.89	4.33	7.48	8.31		
2 Width across	max	45.95	42.80	48.13	45.28	44.14	58.15	49.31
condyles	min	38.87	37.71	42.56	36.08	37.70		
	mean	42.67	40.34	44.48	41.80	40.39		
	st.dev	1.99	1.63	2.31	3.10	1.85		
3 Cranial width	max	67.49	63.12	70.40	69.26	68.03	72.51	61.93
	min	58.54	55.59	50.03	60.59	59.38		
	mean	63.62	59.55	64.40	64.59	62.27		
	st.dev	2.51	2.29	6.91	2.66	2.71		
4 Zygomatic	max	109.56	103.94	106.98	107.36	108.97	113.76	112.64
width	min	85.73	93.33	101.52	90.12	93.61		
	mean	100.44	98.47	105.08	98.93	99.60		
	st.dev	7.96	3.45	2.12	5.14	4.60		
5 Width across	max	81.90	74.02	78.27	86.00	75.36	88.31	80.24
orbits	min	67.59	66.54	74.66	71.98	66.90		
	mean	75.60	70.11	76.27	77.62	70.94		
	st.dev	4.22	2.29	1.34	4.04	3.16		
6 Maxillary	max	66.20	66.08	69.51	68.66	69.42	75.62	73.79
width	min	58.81	58.61	63.56	62.03	59.25		
	mean	61.35	61.65	66.48	64.83	63.34		
	st.dev	2.55	2.30	2.17	2.48	3.15		
7 Premaxillary	max	39.57	34.60	39.00	38.27	33.82	—	30.85
width	min	31.59	27.83	35.02	30.42	27.11		
	mean	35.32	30.65	37.11	34.95	30.90		
	st.dev	2.74	2.17	1.43	2.61	1.87		
8 Palatal	max	61.29	64.00	62.93	66.23	62.64	70.97	69.21
width	min	55.61	55.76	60.03	57.18	56.58		
	mean	58.87	58.19	61.38	61.29	59.31		
	st.dev	2.12	2.25	1.03	2.63	1.80		

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male not aged	Soay Female not aged	Goat Male not aged	Goat Female not aged
No in sample		12 ¹	12 ²	6 ³	10 ⁴	13 ⁵	1	1
9 Length of orbit	max	40.90	39.64	42.67	41.68	39.99	38.37	37.33
	min	37.00	37.25	39.34	37.81	37.18		
	mean	39.33	38.44	41.58	39.68	38.44		
	st.dev	1.42	0.80	1.24	1.20	0.93		
10 Height of orbit	max	40.05	40.57	39.39	40.01	38.71	37.61	33.77
	min	34.99	36.53	36.95	35.96	36.22		
	mean	37.60	37.90	38.19	37.87	37.75		
	st.dev	1.53	1.20	0.96	1.34	0.85		
11 length of toothrow (alveoli)	max	63.24	58.62	64.61	66.58	69.65	68.55	63.58
	min	53.83	50.22	56.99	52.18	53.03		
	mean	58.40	55.37	60.80	59.89	59.74		
	st.dev	3.15	2.20	3.01	4.24	5.27		
12 Height of back of skull	max	47.24	39.92	42.86	43.61	40.46	54.55	43.35
	min	39.46	36.78	38.86	39.86	34.96		
	mean	41.68	38.52	40.74	41.55	38.08		
	st.dev	2.05	0.84	1.69	1.43	1.62		
13 Width between bases of horn cores	max	40.88	45.64	51.80	43.70	58.84	29.67	36.15
	min	26.65	37.80	32.43	31.63	37.79		
	mean	34.64	41.55	41.30	36.77	44.71		
	st.dev	4.89	2.80	7.37	3.75	6.63		

1 10 in sample for condylo-basal length, premaxillary width and the width between the bases of the horn cores.

2 8 in sample for the width between the bases of the horn cores

3 7 in sample for cranial width, and width between the bases of the horn cores; 5 in sample for condylo-basal length and width across orbits.

4 7 in sample for condylo-basal length; 6 in sample for premaxillary width

5 11 in sample for condylo-basal length; 8 in sample for the width between the bases of the horn cores

MANDIBLE

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		11	12	7	20 ¹	3
1 Length from angle	max	157.10	159.50	173.40	166.10	186.70
	min	139.72	99.80	153.70	144.40	167.60
	mean	148.84	148.20	167.87	150.00	180.10
	st.dev	5.49	15.60	6.78	4.87	10.80
2 Length of horizontal ramus	max	109.60	105.96	120.05	118.87	133.11
	min	96.18	97.85	107.98	99.09	127.29
	mean	102.59	102.91	113.07	105.15	129.29
	st.dev	3.84	2.53	4.39	4.22	3.31
3 Length of cheektooth row	max	63.57	62.97	68.79	72.20	78.11
	min	56.63	55.23	58.36	56.63	72.35
	mean	60.17	59.34	64.06	62.65	75.30
	st.dev	2.22	2.27	4.36	3.42	2.88
4 Width of condyle	max	23.76	22.53	22.50	23.11	26.77
	min	19.26	19.18	17.44	18.06	24.21
	mean	21.39	20.88	20.26	20.73	25.13
	st.dev	1.39	0.98	1.61	1.33	1.43
5 Oral height of vertical ramus	max	90.78	94.40	98.11	93.88	108.27
	min	82.29	82.99	85.79	82.80	95.24
	mean	85.75	87.94	91.80	88.30	99.92
	st.dev	3.31	3.55	4.71	3.14	7.25
6 Height of mandible in front of M ₁	max	20.80	19.34	22.54	20.66	23.85
	min	16.61	16.27	18.02	15.95	19.66
	mean	18.88	18.08	20.06	18.27	21.91
	st.dev	1.24	1.03	1.68	1.47	2.11

1 19 in sample for width of condyle

ATLAS

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		12	8	7 ¹	18 ²	2
1 Greatest length	max	53.91	51.74	53.05	55.83	76.74
	min	41.87	42.74	47.75	39.66	64.42
	mean	49.74	45.82	50.10	47.17	70.58
	st.dev	3.25	2.63	1.82	5.22	8.71
2 Greatest width over the wings	max	66.96	60.08	68.12	68.97	96.36
	min	48.75	52.69	53.85	45.86	83.70
	mean	62.08	55.46	62.05	58.06	90.03
	st.dev	5.05	3.04	6.01	7.22	8.95
3 Height of bone	max	36.19	32.46	35.63	36.64	46.05
	min	28.70	29.04	31.23	26.84	43.92
	mean	33.67	30.67	33.10	31.41	44.99
	st.dev	1.95	1.08	1.66	2.77	1.51
4 Width of cranial articular surface	max	46.18	43.01	48.33	46.61	65.51
	min	37.65	39.10	40.52	38.39	58.53
	mean	42.39	40.62	43.54	41.53	62.02
	st. dev	2.18	1.45	2.63	2.33	4.94
5 Width of caudal articular surface	max	44.34	38.82	45.47	43.97	57.77
	min	37.38	35.69	37.78	34.97	53.95
	mean	41.95	37.24	41.76	39.42	55.86
	st.dev	2.25	1.16	2.59	2.66	2.70
6 Ventral length along ventral tuberosity	max	24.42	22.94	24.37	24.56	33.89
	min	19.09	19.80	21.31	17.90	28.51
	mean	22.06	21.15	23.15	21.01	31.20
	st. dev	1.69	1.15	1.27	1.76	3.80

1 5 in sample for greatest width over the wings

2 17 in sample for greatest length and width of cranial articular surface; 16 in sample for greatest width over the wings.

AXIS

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		10	6	7	19 ¹	4 ²
1 Greatest height of bone	max	56.56	42.60	52.69	55.90	76.75
	min	47.69	40.65	42.36	33.54	65.04
	mean	52.26	41.58	49.08	42.26	69.87
	st.dev	2.78	0.65	3.38	6.67	5.27
2 Width of cranial articular surface	max	42.51	38.38	42.27	41.69	54.64
	min	38.05	35.46	37.19	34.57	49.87
	mean	40.64	36.60	39.32	37.94	51.88
	st.dev	1.57	1.25	1.99	2.11	1.99
3 Width of caudal articular surface	max	26.73	20.68	23.63	22.04	34.81
	min	20.46	18.63	18.61	15.24	27.79
	mean	22.82	19.59	21.72	19.56	31.05
	st.dev	2.65	0.84	1.58	1.82	2.99
4 Length including dens	max	52.85	53.84	56.70	5.55	70.10
	min	48.57	48.23	51.99	40.90	63.35
	mean	50.41	50.23	53.39	49.31	67.55
	st.dev	1.47	1.97	1.72	3.07	3.66
5 Length of spinous process	max	43.15	37.20	38.73	44.16	68.33
	min	35.38	31.88	31.77	24.93	58.75
	mean	38.27	33.93	35.84	33.75	62.74
	st.dev	2.46	1.94	2.87	4.19	4.02
6 Width of caudal end of spinous process	max	9.84	5.05	7.65	9.50	12.07
	min	3.02	4.50	4.42	2.64	5.20
	mean	6.69	4.77	5.59	5.32	9.94
	st. dev	2.08	0.19	1.14	1.52	3.23

1 17 in sample for width of caudal articular surface; 18 in sample for length of spinous process.

2 3 in sample for length including dens

SCAPULA

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		10	8	7	20	3
1 Proximal length	max	93.68	83.51	100.04	90.68	119.99
	min	82.94	73.37	75.25	67.03	104.51
	mean	86.91	79.17	89.91	78.62	111.92
	st.dev	2.98	3.87	8.11	5.53	7.76
2 Length of neck	max	19.60	17.00	20.28	19.57	28.46
	min	16.18	15.16	18.47	14.61	27.00
	mean	18.26	16.29	19.35	17.32	27.76
	st.dev	1.12	0.54	0.74	1.41	0.73
3 Height of neck	max	21.20	21.50	26.64	22.21	32.64
	min	18.20	18.20	20.40	16.72	26.91
	mean	19.82	20.15	23.82	19.77	29.28
	st.dev	0.91	1.08	1.87	1.33	2.99
4 Distal length	max	32.09	27.97	32.98	31.06	41.22
	min	29.25	22.52	28.79	26.16	38.03
	mean	30.54	26.91	30.70	28.80	40.00
	st.dev	1.02	1.81	1.51	1.52	1.72
5 Length of glenoid cavity	max	24.64	21.63	25.31	23.02	31.00
	min	21.61	20.22	20.39	19.57	29.63
	mean	22.95	21.05	23.36	21.49	30.48
	st.dev	0.93	0.43	1.81	0.95	0.74
6 Width of glenoid cavity	max	20.89	19.01	21.48	20.49	30.00
	min	18.38	17.01	18.84	17.44	26.55
	mean	19.66	18.09	20.43	19.08	28.43
	st.dev	0.82	0.63	1.02	0.99	1.75
7 Height of bone	max	145.00	141.80	162.50	147.50	184.20
	min	125.90	126.70	140.90	116.10	164.10
	mean	137.49	134.25	151.07	132.22	177.40
	st.dev	6.04	4.55	8.07	8.51	11.50

HUMERUS

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		7	8	8	20	4
1 Length of bone	max	139.80	133.52	148.10	142.59	200.70
	min	133.36	123.99	135.32	117.81	179.00
	mean	137.43	128.24	141.86	128.26	190.50
	st.dev	2.00	3.16	3.58	5.32	9.46
2 Proximal width	max	39.17	35.27	40.06	39.07	53.29
	min	36.72	32.35	35.79	29.51	47.10
	mean	37.72	33.46	38.28	33.69	50.88
	st.dev	0.89	1.07	1.58	2.10	2.77
3 Proximal depth	max	42.20	40.84	45.15	41.23	56.57
	min	38.00	32.88	35.77	33.20	51.84
	mean	40.30	36.25	41.38	36.76	54.11
	st.dev	1.41	2.26	2.99	1.98	2.29
4 Distal width	max	29.69	27.84	30.04	28.85	41.08
	min	27.34	25.13	26.90	23.06	36.79
	mean	28.62	26.27	28.13	25.91	38.82
	st.dev	0.76	0.81	1.23	1.26	2.12
5 Distal depth	max	25.86	22.57	25.39	23.79	31.44
	min	23.13	20.58	22.68	18.71	30.79
	mean	23.76	21.53	23.59	21.41	31.10
	st.dev	0.94	0.76	1.01	1.19	0.33
6 Min shaft width	max	14.83	13.97	15.30	14.45	22.94
	min	13.04	11.95	12.79	10.66	19.19
	mean	13.82	12.79	14.37	12.57	21.00
	st.dev	0.58	0.68	0.92	0.81	1.77
7 Height of coronoid	max	14.40	13.50	14.66	14.10	17.18
	min	13.23	12.31	12.85	11.32	16.17
	mean	13.85	12.75	13.61	12.71	16.57
	st.dev	0.45	0.38	0.68	0.71	0.45

RADIUS

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		7	8	8 ¹	20 ²	4
1 Length of bone	max	147.40	143.80	162.10	155.00	201.50
	min	139.64	133.33	141.20	126.65	172.60
	mean	142.43	137.01	153.83	137.71	185.40
	st.dev	2.69	3.58	6.77	7.82	12.10
2 Proximal width	max	30.92	28.05	31.24	30.88	39.49
	min	28.29	26.43	27.46	25.96	37.76
	mean	29.71	27.31	29.80	27.81	38.92
	st.dev	1.15	0.55	1.10	1.77	0.81
3 Proximal depth	max	16.01	14.54	15.34	15.58	21.41
	min	13.55	13.08	13.96	12.83	19.95
	mean	14.88	13.90	14.65	14.06	20.53
	st.dev	0.74	0.48	0.98	0.77	0.63
4 Distal width	max	28.37	25.90	28.19	28.91	37.66
	min	27.20	24.63	24.50	21.84	35.49
	mean	27.64	25.29	26.66	25.32	36.38
	st.dev	0.41	0.42	1.14	2.15	1.03
5 Distal depth	max	19.87	18.77	21.16	19.47	28.60
	min	17.50	16.50	16.98	15.37	25.26
	mean	18.47	17.32	18.64	16.90	26.75
	st.dev	0.78	0.74	1.24	1.12	1.43
6 Minimum shaft width	max	16.47	15.18	17.33	18.82	25.14
	min	15.42	13.53	14.68	13.10	21.75
	mean	16.03	14.14	16.36	14.95	23.21
	st.dev	0.37	0.52	0.89	1.63	1.46

1 2 in sample for prox depth

2 19 in sample for prox width

ULNA

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		7	8	8	20 ¹	4 ²
1 Length of olecranon	max	40.55	37.50	44.70	43.09	58.28
	min	37.91	31.76	38.95	32.76	49.04
	mean	38.75	34.86	41.64	36.55	52.64
	st.dev	0.87	1.90	1.79	3.30	4.07
2 Depth of olecranon at beak of notch	max	26.54	24.40	28.30	27.39	34.03
	min	24.26	22.54	24.90	21.36	29.46
	mean	25.15	23.49	26.59	24.23	31.46
	st.dev	0.87	0.65	1.19	1.91	2.03
3 Width of proximal articular surface	max	21.14	17.40	19.47	21.67	28.42
	min	16.50	15.47	17.43	14.38	27.08
	mean	18.05	16.63	18.07	16.91	27.87
	st.dev	1.53	0.61	0.75	1.87	0.57
4 Depth of olecranon epiphysis	max	24.24	21.33	23.18	24.19	33.82
	min	21.40	18.20	18.98	17.98	27.87
	mean	22.18	20.19	21.03	20.32	30.05
	st.dev	1.00	1.08	1.54	1.75	3.28
5 Width of olecranon epiphysis	max	10.14	9.49	10.37	11.51	15.63
	min	8.83	7.94	9.28	7.95	14.62
	mean	9.63	8.87	9.75	8.95	15.12
	st.dev	0.52	0.57	0.35	0.84	0.51

1 19 in sample for depth of olecranon epiphysis

2 3 in sample for depth and width of olecranon epiphysis

INNOMINATE BONES

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		7 ¹	13 ²	7 ³	20 ⁴	3 ⁵
1 Length of bone	max	196.50	185.90	204.70	193.70	241.05
	min	171.60	167.10	161.90	161.40	197.10
	mean	185.69	175.95	184.50	179.40	225.14
	st.dev	8.58	4.72	12.60	10.20	20.39
2 Length of symphysis	max	53.97	51.81	54.55	55.70	75.78
	min	44.36	44.83	50.68	42.05	—
	mean	49.43	48.20	52.64	48.94	—
	st.dev	3.78	2.46	1.48	4.46	—
3 Greatest diameter of wing	max	78.98	75.52	76.60	71.34	88.16
	min	61.84	57.28	66.30	57.80	72.92
	mean	67.61	63.61	70.09	65.22	78.65
	st.dev	6.20	4.97	3.88	3.49	8.30
4 Length of ilium	max	104.90	102.10	111.07	107.33	141.02
	min	96.26	92.68	92.79	94.22	123.28
	mean	101.59	98.73	101.56	99.88	132.97
	st.dev	3.14	2.53	6.02	3.95	8.98
5 Length of acetabulum	max	27.96	24.68	27.98	27.87	34.78
	min	24.30	23.28	24.75	22.90	32.07
	mean	25.75	24.03	26.30	25.13	33.64
	st.dev	1.14	0.46	1.20	1.54	1.40
6 Depth of acetabulum	max	7.79	5.37	5.98	8.35	14.08
	min	4.82	2.12	4.50	2.41	12.32
	mean	6.35	3.32	5.12	4.77	13.29
	st.dev	1.07	0.86	0.49	2.00	0.89
7 Width of pelvis across acetabula	max	96.57	100.70	101.12	96.89	111.72
	min	93.03	88.59	95.78	86.35	—
	mean	95.02	93.87	97.75	92.42	—
	st.dev	1.47	3.31	2.16	2.79	—
8 Width of ischial tuberosity	max	102.74	112.76	129.56	108.29	96.60
	min	99.26	95.09	109.36	89.48	—
	mean	100.88	104.27	117.31	99.69	—
	st.dev	1.53	6.89	8.58	4.52	—

1 5 in sample for measurements 7 and 8

2 9 in sample for measurements 7 and 8

3 6 in sample for measurement 2; 5 for measurements 3, 7 and 8

4 18 in sample for measurements 7 and 8

5 1 in sample for measurements 2, 7 and 8; 4 for measurement 1

FEMUR

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		7	8	8	20	5 ¹
1 Length of bone	max	170.60	167.10	184.90	180.40	232.70
	min	161.60	151.90	165.10	150.70	177.10
	mean	166.78	157.62	174.65	159.63	202.70
	st.dev	2.93	4.94	6.96	7.18	27.50
2 Proximal width	max	45.37	40.70	47.17	47.46	58.77
	min	43.22	37.62	42.19	37.35	47.91
	mean	44.09	39.07	44.51	40.57	52.05
	st.dev	0.79	1.15	1.95	2.88	5.10
3 Depth of head of femur	max	20.09	18.51	19.58	20.08	25.76
	min	18.62	17.32	17.62	16.85	20.92
	mean	19.36	17.96	18.78	18.35	24.08
	st.dev	0.57	0.50	0.68	1.04	2.22
4 Distal width	max	37.90	33.92	37.35	38.71	46.17
	min	34.97	31.99	33.71	30.96	39.43
	mean	36.88	32.94	36.10	33.66	42.80
	st.dev	0.95	0.76	1.15	2.11	2.88

FEMUR (cont.)

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		7	8	8	20	5 ¹
5 Minimum width of shaft	max	15.17	14.45	17.71	17.36	22.48
	min	14.26	13.28	14.14	12.41	18.42
	mean	14.66	13.78	15.79	13.98	20.40
	st.dev	0.36	0.39	1.25	1.07	1.95

1 4 in sample for length of bone and proximal width

TIBIA

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		5	8	8 ¹	20	4
1 Length of bone	max	199.40	194.45	219.20	214.40	263.90
	min	189.00	179.17	200.60	174.00	235.80
	mean	193.67	185.28	209.63	186.70	246.30
	st.dev	3.79	4.61	7.79	10.30	12.60
2 Proximal width	max	40.05	37.76	41.70	41.52	51.09
	min	38.72	34.74	38.69	33.41	48.66
	mean	39.42	36.19	40.13	36.63	49.62
	st.dev	0.62	0.94	1.00	2.09	1.18
3 Proximal depth	max	45.28	40.16	42.55	39.03	46.95
	min	38.50	34.20	37.50	31.22	40.69
	mean	41.74	38.44	40.08	34.52	44.19
	st.dev	2.86	2.05	1.62	2.43	2.76
4 Dorsal width	max	25.40	25.13	26.60	25.96	32.11
	min	24.14	22.30	24.20	21.20	30.44
	mean	24.75	23.59	24.86	23.01	31.33
	st.dev	0.51	1.02	0.85	1.20	0.78
5 Distal depth	max	20.53	19.16	20.98	20.16	23.02
	min	18.96	17.94	18.66	17.22	22.48
	mean	19.62	18.48	19.74	18.31	22.76
	st.dev	0.64	0.37	0.74	0.86	0.22
6 Minimum width of shaft	max	14.22	14.26	15.70	16.56	19.73
	min	13.33	12.25	13.80	12.07	17.81
	mean	13.84	12.80	14.86	13.23	18.57
	st.dev	0.35	0.63	0.75	1.07	0.83

1 7 in sample for length of bone, prox width and prox depth

PATELLA

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		5	4	7	19	4
1 Length of bone	max	29.73	26.96	30.23	28.83	39.60
	min	28.06	25.22	25.59	23.39	36.00
	mean	28.92	26.39	28.12	25.62	37.53
	st.dev	0.76	0.82	1.75	1.33	1.50
2 Proximal width	max	21.51	19.25	21.80	20.63	25.90
	min	18.77	17.24	19.12	16.66	22.94
	mean	20.40	18.25	20.52	18.52	24.98
	st.dev	1.03	0.84	1.01	1.08	1.37

TALUS

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		9	8	7	20	3
1 Length of bone	max	28.67	25.87	28.20	30.53	34.13
	min	25.92	23.72	25.13	22.59	30.66
	mean	26.60	24.53	26.63	24.49	32.66
	st.dev	0.86	0.75	1.16	1.65	1.79

TALUS (cont.)

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
2 Distal width	max	18.24	17.11	18.28	19.94	21.94
	min	16.66	15.74	16.20	14.80	20.37
	mean	17.21	16.18	17.36	16.11	21.35
	st.dev	0.49	0.47	0.66	1.06	0.86

CALCANEUM

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		7	7	7	20 ¹	4 ²
1 Length of bone	max	53.37	51.88	57.18	53.67	67.71
	min	51.34	47.90	52.68	45.09	64.42
	mean	52.22	49.91	54.57	49.72	66.27
	st.dev	0.68	1.60	1.92	2.19	1.68
2 Width of bone	max	19.89	18.60	20.42	19.91	25.05
	min	17.66	17.29	15.12	15.75	23.14
	mean	18.66	17.94	17.64	17.72	24.10
	st.dev	0.75	0.48	2.05	1.16	0.80
3 Length of central articular condyle	max	13.01	11.78	12.51	12.70	13.33
	min	10.76	10.47	9.25	10.10	12.86
	mean	11.82	11.20	10.45	11.37	13.12
	st.dev	0.69	0.53	1.31	0.60	0.19
4 Length of lateral process below condyle	max	9.90	9.70	11.65	10.30	13.96
	min	6.28	5.81	8.78	7.52	10.18
	mean	7.76	6.78	10.00	8.74	12.39
	st.dev	1.39	1.33	0.89	0.69	1.61

1 18 in sample for length of bone

2 3 in sample for length of bone

METACARPAL

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		8	8	8 ¹	20	3
1 Length of bone	max	125.47	118.69	134.57	122.90	125.31
	min	113.52	113.16	118.90	102.82	116.34
	mean	119.93	116.15	127.54	114.18	121.32
	st.dev	4.44	2.30	5.07	5.34	4.57
2 Proximal width	max	22.77	21.19	22.99	22.39	29.83
	min	20.53	19.24	20.54	18.25	29.59
	mean	21.74	20.20	21.86	19.91	29.69
	st.dev	0.76	0.65	0.79	1.10	0.13
3 Proximal depth	max	16.71	19.16	17.06	16.85	19.96
	min	15.32	14.58	15.24	13.53	19.05
	mean	16.00	15.56	16.02	14.80	19.54
	st.dev	0.52	1.49	0.62	0.81	0.46
4 Distal width	max	25.12	22.96	25.22	23.70	33.41
	min	22.12	21.22	23.83	19.19	33.05
	mean	23.70	21.92	24.25	21.70	33.29
	st.dev	0.93	0.62	0.44	1.17	0.21
5 Distal depth	max	16.54	15.16	16.13	16.61	19.96
	min	14.94	14.39	14.43	13.36	18.68
	mean	15.71	14.78	15.37	14.64	19.38
	st.dev	0.49	0.31	0.65	0.92	0.65
6 Minimum shaft width	max	15.04	13.65	14.50	15.12	22.07
	min	13.35	11.88	12.86	11.50	21.82
	mean	14.10	12.59	13.79	12.82	21.95
	st.dev	0.63	0.66	0.56	1.01	0.13

METACARPAL (cont.)

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		8	8	8 ¹	20	3
7 Depth of medial trochlear condyle	max	11.12	9.74	11.21	11.13	11.72
	min	9.72	9.32	9.72	9.11	11.33
	mean	10.54	9.67	10.43	10.04	11.53
	st. dev	0.46	0.14	0.58	0.52	0.20

1 7 in sample for depth of medial trochlear condyle

METATARSAL

		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		8	8	8 ¹	20	4
1 Length of bone	max	136.01	134.17	148.20	137.75	141.27
	min	122.77	123.15	132.08	112.26	128.18
	mean	128.66	126.59	140.58	124.47	133.05
	st.dev	4.54	3.75	5.73	6.49	6.16
2 Proximal width	max	20.10	18.62	20.43	19.40	24.07
	min	18.01	17.10	18.27	16.90	23.97
	mean	19.01	17.83	19.46	17.99	24.04
	st. dev	0.71	0.59	0.78	0.69	0.04
3 Proximal depth	max	20.39	18.81	20.89	20.05	24.06
	min	19.14	17.56	18.56	16.90	22.78
	mean	19.79	18.23	19.65	18.12	23.60
	st.dev	0.50	0.41	0.79	0.84	0.57
4 Distal width	max	24.05	21.86	24.02	23.45	31.29
	min	21.39	20.38	22.54	20.07	28.40
	mean	22.63	21.07	23.32	21.30	30.14
	st.dev	0.84	0.57	0.57	0.98	1.27
5 Distal depth	max	16.18	14.92	16.24	15.53	19.43
	min	14.63	13.98	14.31	13.61	18.23
	mean	15.42	14.53	15.37	14.43	18.63
	st.dev	0.48	0.33	0.69	0.54	0.54
6 Minimum width of shaft	max	12.77	11.77	12.79	13.33	17.77
	min	11.39	10.41	10.76	9.63	16.93
	mean	11.87	10.97	12.09	11.05	17.45
	st.dev	0.51	0.48	0.67	0.81	0.36
7 Depth of medial trochlear condyle	max	10.29	9.37	10.41	10.36	11.56
	min	9.00	8.74	9.10	8.60	10.81
	mean	9.65	9.13	9.79	9.33	11.14
	st.dev	0.43	0.21	0.60	0.49	0.32

1 7 in sample for depth of medial trochlear condyle

PHALANX 1

		FORE		HIND		FORE/HIND		
		Soay Male aged	Soay Female aged	Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		8	5	8	6	3	4	20
1 Length of bone	max	36.41	32.85	35.87	33.28	35.69	35.37	34.00
	min	32.26	31.34	33.59	31.44	33.84	33.99	29.45
	mean	34.74	32.01	34.30	32.24	34.93	34.66	31.43
	st.dev	1.37	0.75	0.72	0.69	0.97	0.68	1.11
2 Proximal width	max	12.76	11.28	11.74	11.74	12.34	12.72	11.66
	min	11.29	10.55	9.89	9.89	12.04	11.51	9.63
	mean	11.90	10.95	11.08	10.51	12.20	11.89	10.67
	st.dev	0.41	0.31	0.54	0.66	0.15	0.56	0.60
3 Proximal depth	max	15.54	13.58	14.54	13.69	14.19	14.47	14.25
	min	13.96	13.14	13.40	12.77	13.17	13.36	11.93
	mean	14.54	13.39	14.00	13.12	13.54	13.95	12.87
	st.dev	0.61	0.20	0.46	0.34	0.57	0.47	0.67

PHALANX 1 (cont.)		FORE		HIND			FORE/HIND	
		Soay Male aged	Soay Female aged	Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Castrate aged	Goat Male/Female not aged
No in sample		8	5	8	6	3	4	20
4 Distal width	max	11.92	10.28	10.35	10.63	11.68	11.42	11.10
	min	10.36	10.02	9.06	8.78	10.56	10.12	8.79
	mean	11.05	10.14	9.90	9.23	11.28	10.82	9.75
	st.dev	0.56	0.10	0.45	0.70	0.63	0.56	0.65
5 Minimum shaft width	max	10.27	9.33	9.52	8.98	10.20	10.78	10.11
	min	9.25	8.42	8.06	7.86	9.35	9.19	7.39
	mean	9.77	8.83	8.69	8.36	9.79	9.79	8.61
	st.dev	0.40	0.40	0.47	0.45	0.43	0.73	0.68

PHALANX 2

		FORE		HIND			FORE/HIND	
		Soay Male aged	Soay Female aged	Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Castrate aged	Goat Male/Female not aged
No in sample		8	5	9 ¹	4	3	4	20
1 Length of bone	max	22.89	20.70	22.07	20.23	21.80	21.26	20.52
	min	19.96	18.94	20.14	18.86	20.51	18.64	16.73
	mean	21.62	19.68	21.14	19.45	20.97	19.97	18.54
	st.dev	0.95	0.78	0.69	0.60	0.72	1.08	1.02
2 Proximal width	max	11.95	10.45	11.00	9.52	11.39	11.98	11.12
	min	10.75	9.90	9.63	9.07	10.00	10.12	8.97
	mean	11.11	10.25	10.25	9.23	10.53	10.74	10.01
	st.dev	0.37	0.21	0.48	0.21	0.75	0.84	0.63
3 Proximal depth	max	13.04	11.93	11.61	10.91	12.51	12.26	12.51
	min	11.42	10.83	10.36	10.08	11.49	11.52	10.19
	mean	12.27	11.51	11.14	10.29	12.02	11.92	11.32
	st.dev	0.63	0.44	0.44	0.42	0.51	0.33	0.64
4 Distal width	max	10.54	8.89	8.88	8.06	9.25	10.20	9.07
	min	8.79	8.41	8.05	7.50	8.16	8.54	7.01
	mean	9.69	8.75	8.47	7.80	8.80	9.21	8.16
	st.dev	0.61	0.20	0.26	0.23	0.57	0.70	0.58

1 8 for prox depth

PHALANX 3—HOOF CORE

		FORE/HIND				
		Soay Male aged	Soay Female aged	Soay Castrate aged	Soay Male/Female not aged	Goat Male/Female not aged
No in sample		9	7	6	20	2
1 Length of bone	max	27.16	26.77	29.84	27.12	34.61
	min	23.33	24.10	26.51	21.63	32.21
	mean	25.50	25.16	27.64	24.23	33.41
	st.dev	1.30	0.95	1.23	1.55	1.70
2 Height of bone	max	15.30	14.72	16.14	15.89	19.35
	min	13.05	13.99	14.67	12.46	18.06
	mean	14.59	14.34	15.40	14.22	18.71
	st.dev	0.82	0.25	0.58	0.93	0.91